RELATIONSHIPS BETWEEN PLANT PRODUCTIVITY AND SOIL CONDITIONS IN ALPINE TUNDRA OF SOUTHERN YUKON TERRITORY, CANADA

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ABSTRACT

Climate change is predicted to significantly alter ecosystem functioning and species distributions across the globe. Arctic and alpine areas are experiencing a faster rate of temperature increase as compared to other environments, and are expected to be highly sensitive to climate change. Current research and modeling predicts changes in plant productivity and ultimately northward biome shifts; however, the exact mechanisms that will drive these changes are still uncertain. Previous studies suggest that changes in soil temperature, not air temperature, regulate many aspects of plant productivity in cool environments through the indirect effects of temperature on nutrient availability. This research focused on how soil properties are linked to plant productivity in northern environments, through an assessment of soil temperature, soil nitrogen, soil moisture, snow depth, and plant productivity near Whitehorse, Yukon, Canada. The effects of soil warming on soil nitrate and ammonium concentrations, and plant growth, and the effects of ammonium-nitrate fertilization on plant growth, were assessed in an experimental warming and fertilization study. Relationships between mean soil temperature, soil temperature coefficient of variation, total soil nitrogen, soil moisture, snow depth, and plant productivity were examined through field observations along a natural vegetation gradient.

In both of these studies I found that plant productivity showed the strongest response to soil nitrogen. In the experimental study, the only species to respond to the experimental manipulations, *Carex microchaeta*, showed the strongest response of leaf length to warming + fertilization and a stronger response to fertilization than warming, and in the gradient study, soil nitrogen showed the strongest patterns of covariance with plant productivity. Nitrogen

having the strongest relationship with plant productivity, and leaf traits showing the greatest responses to fertilization, was consistent with the theory that nitrogen availability is the strongest factor limiting plant growth in both arctic and alpine tundra plants. I found that soil moisture had the second strongest correlation with plant productivity in the gradient study, and that soil moisture was also strongly correlated to total soil nitrogen levels. Tall shrubs were consistently different from other vegetation types, with increased productivity as compared to other vegetation types at all levels of environmental factors in the gradient study, and the strongest relationship with tall shrub habitat productivity was not soil nitrogen but mean soil temperature.

While I could not infer causality from the descriptive study of the landscape, the strong relationship of soil moisture with both plant productivity and soil nitrogen indicated that changes in precipitation resulting in increased soil moisture could be an important determinant of future plant productivity at this alpine site. However, my results also suggested that increasing temperatures will result in tall shrub habitats showing greater increases in productivity than other vegetation types. The positive correlations between most environmental factors and plant productivity indicated that increases in plant productivity could be expected with the environmental changes that have been predicted with climate change. Increases in temperature, precipitation causing increased soil moisture, and nitrogen availability will likely result in higher plant productivity at this alpine site, but the relative increases in plant productivity between different plant groups will depend on which environmental factor experiences the greatest changes.

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

LIST OF ABBREVIATIONS

ANOVA: Analysis of variance

HSD: Honestly significant difference

ITEX: International Tundra Experiment

KCl: Potassium chloride

LAI: Leaf area index

LM: Leaf dimension measurements

MANOVA: Multivariate analysis of variance

NH_4NO_3: Ammonium-nitrate

NH_4^+: Ammonium

NO_3^-: Nitrate

OTC: Open topped chamber

PCA: Principle components analysis

SLA: Specific leaf area

UV: Ultraviolet

PREFACE

This thesis is organized into two manuscript-style data chapters based on the two studies performed during the degree, a natural gradient study and an experimental study. The two data chapters are preceded by a general introduction and followed by a concluding chapter.

1.0 INTRODUCTION

1.1 ARCTIC CLIMATE CHANGE AND PLANT PRODUCTIVITY

The Earth is currently in a warming period and conservative estimates of at least a 0.6°C increase in global temperatures is predicted for the next 100 years (Solomon et al. 2007). Continuing increases in global temperature are of increasing importance across the globe, due to the many predicted effects on global ecosystems, including changes to species ranges, terrestrial carbon storage, water availability, and species extinctions (Parry et al. 2007). However, not all parts of the world will experience similar rates of climate change. Arctic and alpine environments are of particular concern, due to their greater rates of atmospheric warming as compared to the rest of the world. Over the last 100 years the rate of Arctic warming has been twice the global average, with greater increases during winter and spring (ACIA 2005, Solomon et al. 2007). Future increases in temperature are projected to be more pronounced in autumn and winter, with increases in the mean annual temperature of approximately 2.5°C north of 60° N in the next 50 years (ACIA 2005, Solomon et al. 2007). Climate data in the Canadian Arctic is sparse prior to 1950 so little is known about atmospheric warming in the first part of the 20th century (Furgal and Prowse 2008). Since the 1950's, increases in the mean annual temperature across the Canadian Arctic showed greater rates of warming in the west (Furgal and Prowse 2008).

Altered patterns of precipitation are also expected to occur with climate change in addition to increasing temperatures (ACIA 2005, Solomon et al. 2007). During the twentieth century precipitation across the Arctic increased by 1.4% per decade, while in the Canadian Arctic the greatest increases in precipitation were in the far north, with increases of 16 to 25% since the 1950's (Furgal and Prowse 2008). There is greater uncertainty in predicted increases in

precipitation than in temperature, with global annual precipitation increasing between 1.4 to 4.7% while precipitation north of 60°N is expected to show increases of 7.5 to 18.1% by the end of the 21st century (ACIA 2005). This predicted increase in precipitation will be more pronounced in autumn and winter, which is linked with increasing air temperatures allowing for greater transportation of water vapour from lower to higher latitudes (ACIA 2005). Estimated increases in precipitation across the Canadian Arctic are consistent with the spatial pattern of recent precipitation changes, with the greatest increases predicted for the far north (Furgal and Prowse 2008).

The predicted changes in temperature and precipitation will also affect other abiotic and biotic factors in the environment. Some direct abiotic changes from air temperature and precipitation include changes in soil temperature and soil moisture. The cryosphere is also particularly sensitive to the effects of climate change (ACIA 2005, Furgal and Prowse 2008). Some of these changes include reductions in the extent of snow cover, earlier snow and ice melt, increased permafrost temperatures, and increased active layer depths (ACIA 2005, Furgal and Prowse 2008). Increased winter temperatures result in increases in the proportion of winter precipitation falling as rain and reduction of snow cover extent and duration (ACIA 2005). The increase in winter precipitation is unlikely to compensate for the reduction in snow cover due to increased temperature (Lapp et al. 2005). This interaction between increased temperature and precipitation in winter has already been seen in the western Canadian Arctic and Alaska in a decrease in both extent and duration of snow cover despite an increase in winter precipitation (ACIA 2005). The reduction in snow cover extent and duration could result in decreases in winter near surface soil temperatures due to a loss of the insulating snow layer

and also to colder soil temperatures experienced by plants at the beginning of the growing season due to earlier snow melt (Zhang 2005, Wipf and Rixen 2010). Earlier snow melt would move the growing season to an earlier and likely colder time of year (Wipf and Rixen 2010). The combination of increasing air temperatures and changing snow cover has lead to increasing permafrost temperatures, permafrost degradation, and increasing active layer thickness (Lemke et al. 2007). Changing soil temperatures also affect permafrost and active layer depth, which can be affected by many factors including air temperature and the timing, duration, and thickness of snow cover (Anisimov et al. 1997, Zhang 2005). Permafrost and the active layer can be important in terms of plant rooting; temperatures are reduced in the rooting zone in areas with permafrost close to the surface, and a shallow active layer can also limit the rooting zone itself by reducing the depth that roots can grow (Jackson et al. 1996, Hinkel et al. 2001).

Plants in colder climates are sensitive to increasing temperatures (Aerts *et al.* 2006) and since the Arctic is expected to undergo more extreme temperature increases than other areas of the globe, it is likely that changes to plant community productivity and composition will occur in these cold biomes. The phenology of arctic plants can also be expected to change, such as changes to timing of bud burst with changes to snowmelt timing (Wipf and Rixen 2010), earlier bud burst and accelerated growth due to warming (Aerts et al. 2006), and delayed flowering with increased nitrogen (Smith et al. 2012). Dynamic vegetation models have predicted changes in northern plant community composition, such as the loss of endemic species (ACIA 2005) and increases in shrub abundance (Epstein *et al.* 2000), as well as northward biome shifts (e.g., Kittel *et al.* 2000, Kaplan *et al.* 2003, Gonzalez *et al.* 2010). Some of these changes in plant communities are already being observed across the arctic. In Alaska

there is evidence of an initiating boreal forest biome shift (Beck *et al.* 2011), while in the Alaskan, Canadian, and Russian Arctic tundra, increasing shrub abundance has been observed (Myers-Smith *et al.* 2011). However, changes in the productivity of extant plant species are expected to occur prior to shifts in community composition. These changes in plant productivity can be due to both direct and indirect effects of climate change.

Arctic and alpine plants are adapted to short, cool growing seasons and have the ability to maintain physiological processes at temperatures that inhibit plants from more temperate climates (Chapin 1983). Some of the processes that are directly affected by temperature include increased photosynthesis, growth rate, and nutrient uptake (e.g., Chapin 1983, Bassirirad 2000, Rustad *et al.* 2001). Recent studies have indicated that soil temperature may play a more important role than air temperature in regulating changes in plant productivity (e.g., Brooker and van der Wal 2003, van Wijk *et al.* 2003, Natali *et al.* 2012). Warming studies, of both air and soil, have indicated that an increase in vascular plant aboveground biomass can be expected with increased temperatures in arctic environments (e.g., Rustad *et al.* 2001, Walker *et al.* 2006, Elmendorf *et al.* 2012a), particularly graminoids and deciduous shrubs (e.g., Chapin *et al.* 1995, Dormann and Woodin 2002, Walker *et al.* 2006). These changes in plant productivity have been tied to the indirect effects of temperature on nutrient availability, not simply warmer temperatures alone (e.g., Chapin 1983, Chapin *et al.* 1995, Brooker and van der Wal 2003).

Nutrient levels are often lower in tundra environments as compared to more temperate environments with relatively more nutrients locked away in organic matter within tundra soil. The low available nitrogen in tundra soils is a result of slow decomposition and mineralization

due to low soil temperature and moisture (e.g., Shaver *et al.* 1992, Jonasson *et al.* 1996, Jonasson *et al.* 1999a). Nitrogen is one of the most limiting nutrients for plant growth in arctic and alpine tundra (e.g., Shaver and Chapin 1980, Nadelhoffer *et al.* 1992, Atkin 1996). Arctic plants are able to take up both organic monomers and inorganic nitrogen (Schimel and Bennett 2004), but only small amounts of total soil nitrogen are present in inorganic or available organic forms (Callaghan *et al.* 2004). Both gradient studies and nitrogen fertilization studies in alpine and arctic tundra have shown that productivity responds positively to increased soil nitrogen and nitrogen cycling, although individual species show responses of different magnitudes (e.g., Shaver and Chapin 1980, Fisk *et al.* 1998, Jonasson *et al.* 1999b). Increased net nitrogen mineralization has been associated with increased soil temperatures across arctic sites (e.g., Hartley *et al.* 1999, Rustad *et al.* 2001, Aerts *et al.* 2006), likely due to increased microbial enzyme activities at higher temperatures (Kosh *et al.* 2007). Plant available nitrogen, and thus plant productivity, could increase due to this indirect effect of climate change on nitrogen mineralization. Graminoids are often the first functional group to respond to nitrogen addition in both arctic and alpine tundra, generally followed by increases in deciduous shrubs in later years (e.g., Press *et al.* 1998, Shaver *et al.* 2001, Haugwitz and Michelsen 2011).

An increase in the proportion of precipitation falling in winter will alter the soil moisture and nutrient inputs experienced by plants during the early growing season (Buckeridge and Grogan 2010). Changes in soil moisture and snow cover will indirectly affect plant productivity principally through their effects on both soil temperature and soil nutrients (e.g. Fisk *et al.* 1998, Callaghan *et al.* 2004, Jonas *et al.* 2008), discussed in further detail below. In addition to the indirect effects of precipitation on vegetation through changes to soil temperature and

nutrients, soil moisture and snow cover can directly affect plant growth. It has long been understood that moisture directly affects plant productivity through its use in vital processes such as photosynthesis and transport (Veihmeyer and Hendrickson 1950, Taiz and Zeiger 2006). Snow can directly affect plant growth through protection from winter desiccation and wind abrasion, as well as potentially reducing the growing season through later melt dates (Sturm *et al.* 2001, Larsen *et al.* 2007). A meta-analysis of snow manipulation experiments indicated that plant groups respond differently to changes in snow cover, with forbs showing increased productivity and abundance with delayed snow melt and increased snow cover, while graminoids showed decreased productivity and deciduous shrubs showed little to no effect (Wipf and Rixen 2010).

1.2 RELATIONSHIPS BETWEEN THE ENVIRONMENT AND VEGETATION

The environmental factors discussed above that affect plant growth do not act independently of each other, and vegetation can in turn modify the environmental factors. These feedbacks create a complex system of interactions that result in a mosaic of different associations between plant productivity, soil temperature, soil moisture, soil nitrogen, and snow cover across the landscape.

Climate change is frequently viewed mainly as increased air temperatures; however, changes in air temperature often cause corresponding changes in soil temperature due to conductive heat transfer (Beltrami and Kellman 2003). Soil temperature is also affected by incident solar radiation, which can by modified by a variety of other factors that alter albedo and shading, such as vegetative cover and snow cover (Zhang *et al.* 2001). Vegetation serves as a shading and insulating layer, reducing incoming solar radiation (Blok *et al.* 2010) as well as

reducing the convective heat transfer of warmer air above the vegetation to cooler air within the canopy (Wang *et al.* 2009). Thus the presence of vegetation can modify summer soil temperatures. Snow cover similarly affects winter soil temperatures, but results in increased soil temperatures as compared to exposed sites (Wundram *et al.* 2010). The snow insulates the soil from the colder air temperatures, such that greater snow depths result in more insulation and thus higher winter soil temperatures. Snow cover and vegetation cover also interact to affect soil temperatures. Vegetation tends to trap snow, protecting it from being redistributed by the wind (Pomeroy *et al.* 2006). Thus sites with tall vegetation have a tendency to moderate soil temperatures in both summer and winter, and experience both cooler summer temperatures and warmer winter temperatures.

Evaporative cooling is also an important determinant of summer soil temperatures, which can be affected by both vegetative cover and soil moisture (Zhang *et al.* 2001). Soil moisture can reduce soil temperature through evaporative cooling (Zhang *et al.* 2001). However the presence of vegetation can buffer changes in soil temperature by shading the soil from direct solar radiation and at the same time reducing wind, thus reducing evaporation and evaporative cooling (Heijmans *et al.* 2001, Wang *et al.* 2009). Temperatures in arctic and alpine tundra are generally lower than optimal for plant photosynthesis and growth (Chapin 1983), which is supported by findings that increased arctic soil temperature is associated with increased plant productivity (e.g., Hartley *et al.* 1999, Brooker and van der Wal 2003, Natali *et al.* 2012). Thus, at the same time that vegetation affects soil temperature, soil temperature also affects vegetation. Increases in soil temperature may be reinforced by the presence of vegetation and

cause increased vegetation productivity, resulting in a system of feedbacks which could moderate soil temperatures in a direction favorable for plant growth.

Soil nitrogen turnover is affected by soil temperature, as well as by many of the same factors that affect soil temperature including soil moisture, snow cover, and vegetative cover (e.g., Jonasson *et al.* 1999a, Wu *et al.* 2006, Currie *et al.* 2010). External inputs of nitrogen are quite low in the arctic, in the form of precipitation, atmospheric deposition, and nitrogen fixation (Chapin 1983). Thus increases in plant available nitrogen will most likely occur through changes in the rates of nitrogen cycling. Increased nitrogen mineralization (e.g., Hartley *et al.* 1999, Rustad *et al.* 2001, Aerts *et al.* 2006) and immobilization (Sorensen *et al.* 2008a & 2008b) has been associated with increased soil temperatures across arctic sites. Thus, the amount of plant available nitrogen is due to a balance of microbial uptake and release. However, across many arctic sites it has been found that overall increased soil temperatures results in increased net nitrogen mineralization, and thus in plant available inorganic nitrogen (Rustad *et al.* 2001). Decomposition and nitrogen mineralization tend to be greatest at moderate levels of soil moisture, with low levels of soil moisture inhibiting microbial activity, while very high soil moisture levels are also inhibiting due to anaerobic conditions (Nadelhoffer *et al.* 1992, Prado and Airoldi 1999). Snow cover increases winter soil temperatures, as discussed above, and increases the availability of unfrozen water, allowing for increased nitrogen mineralization in winter (Borner *et al.* 2008). Increased snow cover can also provide a flux of nitrogen from lysing microbes, as well as increased moisture during thaw events (Buckeridge and Grogan 2010).

1.3 CLIMATE CHANGE RESEARCH

Climate change research often consists of various environmental manipulations including, but not limited to, air and soil temperature, carbon dioxide concentrations, nutrient levels, summer and winter precipitation, and enhanced ultraviolet (UV-B) radiation (e.g Shaver and Chapin 1980, Heijmans *et al.* 2001, Phoenix *et al.* 2001, Borner *et al.* 2008, Natali *et al.* 2012). Many climate change studies focus on manipulating temperature; however, few studies have specifically assessed the effects of manipulating soil temperature on plant productivity in arctic or alpine tundra (but see Hartley *et al.* 1999, Brooker and van der Wal 2003, Natali *et al.* 2012). Temperature manipulations can be classified under active or passive systems (Aronson and McNulty 2009). Passive systems generally alter temperatures by trapping solar energy and reducing heat loss, while active systems require external heat sources (Marion *et al.* 1997, Aronson and McNulty 2009). Passive systems are commonly used in northern and alpine studies due to the lack of reliable power sources (Aronson and McNulty 2009, Johnstone *et al.* unpublished ms.).

A common passive soil warming technique is open-topped chambers (OTCs) that are used in the International Tundra Experiment (ITEX). OTCs often have variable effects on both air and soil temperature and can cause many secondary effects on factors such as wind speed, carbon dioxide concentrations, and moisture (Marion *et al.* 1997). Active warming systems, such as infrared heating lamps and buried heating cables, generally have a more consistent effect on temperatures (Aronson and McNulty 2009). Active heating systems have a high power demand and require complex control systems to maintain target temperatures. Buried heating cables require disturbance of the vegetation and soil to install, but they are in direct contact with the

soil and so have a more direct effect on soil temperatures. Buried heating cables are also useful to separate the effects of air and soil temperatures since buried cables do not affect air temperatures. Infrared heating lamps are set up above the vegetation, and thus heat both air and soil. However, the vegetation between the heating lamps and the soil may reduce the ability of the lamps to increase soil temperatures (Aronson and McNulty 2009).

Other climate change studies attempt to extrapolate what might occur under conditions of climate change by examining naturally occurring environmental gradients (Dunne *et al.* 2004). This is done with the assumption that ecosystem interactions are the same across both space and time. This can sometimes be the case, such that long-term experimental studies found that the plant responses to temperature manipulations are similar to what can be found along a natural environmental gradient (Chapin *et al.* 1995). However, not all substitutions of space for time can be assumed to be accurate due to problems such as local adaptations altering the plant-environment interactions and faster rates of climate change than what was experienced historically along a natural gradient (Dunne *et al.* 2004). The differences between experimental and natural gradient studies are many, but a common difference is the scale at which ecosystem interactions are studied (Dunne *et al.* 2004). Experimental studies often require intensive inputs of money and infrastructure to implement the environmental manipulation (Aronson and McNulty 2009), and thus are generally smaller in scale than natural gradient studies (Dunne *et al.* 2004). Combining the results of experimental and natural gradient studies at different spatial scales can lead to increased understanding of underlying ecosystem processes. As well, the assessment of natural gradients is an important part of being able to

more accurately apply the results from an experimental study through both space and time (Dunne *et al.* 2004).

Determining the correlations along a naturally occurring gradient provides additional information about long-term relationships that could prove useful in the interpretation of the short-term responses to the experimental study. For example, if both experimental and gradient studies find similar relationships between factors, then it could indicate that the relationship in question is consistent across both time and space, whereas if they discover conflicting relationships it could indicate that the relationship is either context-dependent or dynamic across space or time (Dunne *et al.* 2004). With regards to this study, the response of plant productivity to soil temperature and nitrogen availability, finding similar responses in both the short-term experimental study and the gradient study could indicate that the vegetative response to climate change persists in the long-term. Finding different responses could also help determine the relative importance of soil temperature and nitrogen availability on productivity as compared to other factors present on the landscape.

1.4 OBJECTIVES

A mechanistic understanding of whole ecosystem processes is required to adequately predict future responses to climate. Numerous studies have stressed the importance of indirect effects of climate change via changes in soil processes (e.g., Shaver and Chapin 1980, Jonasson *et al.* 1999b, van Wijk *et al.* 2003), but there are still gaps in our understanding of such effects. Much of the previous research on climate effects on vegetation have focused on changes in air temperatures; this study will provide a new contribution by specifically assessing how changes in the soil environment affect plant dynamics. The goal of the research presented here was to

determine the relationships between soil temperature, soil nitrogen, and plant productivity. This was done using a natural vegetation gradient to determine the current patterns along the landscape and an active soil warming and fertilization experiment to determine the possible initial responses that could result from a warming climate.

Specifically, the principle objectives of this thesis were to: a) test for the relationship between soil temperature and soil nitrogen, b) test for the relationships between both soil temperature and soil nitrogen with plant productivity, and c) examine the relative importance of soil temperature and soil nitrogen as compared to soil moisture and snow cover in determining plant productivity on the natural landscape. The experimental study uses a unique solar powered warming system specifically designed for remote locations and to increase only soil temperatures. The natural gradient study provides insight into how plant productivity is related to various soil properties, and will also be integrated with the experimental study to provide further information on how these underlying relationships vary across both space and time.

2.0 PATTERNS OF PLANT PRODUCTIVITY ALONG A NATURAL VEGETATION GRADIENT

2.1 INTRODUCTION

Arctic and alpine environments have been experiencing greater rates of temperature change than other areas of the world, with the rate of Arctic warming at twice the global average over the last 100 years (ACIA 2005, Solomon et al. 2007). Arctic plant communities are expected to be highly sensitive to climate change, and biome shifts are predicted as a result (Epstein *et al.* 2000, ACIA 2005). However, changes in the productivity of extant plant species can be expected to occur prior to the predicted shifts in community composition. To understand the mechanisms for how these changes are going to occur, we must first determine the underlying relationships between environmental factors and plant productivity that are currently present on the landscape. Previous studies in both alpine and arctic tundra indicate that changes in soil temperature play a more important role in regulating plant productivity than air temperature, because of indirect effects on nutrient availability (e.g., Chapin 1983, Chapin *et al.* 1995, Brooker and van der Wal 2003). Soil moisture and snow cover are also important regulators of plant productivity in tundra ecosystems, principally through their effects on both soil temperature and soil nutrients (e.g., Fisk *et al.* 1998, Callaghan *et al.* 2004, Jonas *et al.* 2008). This study focuses on the relationships between soil temperature, soil nitrogen, soil moisture, snow cover, and plant productivity in alpine tundra along a natural vegetation gradient.

Climate change is frequently viewed mainly as increased air temperatures, however changes in air temperature often cause corresponding changes in soil temperature due to conductive heat transfer (Beltrami and Kellman 2003). Soil temperature is mainly a result of incident solar radiation, which can by modified by a variety of other factors that alter albedo

and shading, such as vegetative cover and snow cover (Zhang *et al.* 2001). Evaporative cooling is also an important determinant of summer soil temperatures, which can be affected by both vegetative cover and soil moisture (Zhang *et al.* 2001). The interactions of these factors result in heterogeneous soil temperatures across the landscape, both spatially and temporally (Zhang *et al.* 2001).

Soil temperature fluctuations tend to be reduced under vegetative cover, with maximum temperatures reduced due to shading (Blok *et al.* 2010), and minimum temperatures increased due to the vegetation acting as an insulating layer that reduces the air-soil heat transfer (Wang *et al.* 2009). Snow cover also acts as an insulating layer and raises the minimum temperature in winter (Wundram *et al.* 2010). Taller vegetation can have greater insulative properties than shorter vegetation in both summer and winter. If tall vegetation corresponds to thicker vegetative cover, then there is greater shading during the summer. Additionally, taller vegetation tends to trap more snow than short stature vegetation (Pomeroy *et al.* 2006) and thus has greater insulative effects on soil temperature. Therefore tall vegetation generally experiences less extreme seasonal temperature fluctuations than shorter stature vegetation.

Soil moisture affects the thermal conductivity of soils, increasing with increasing moisture content (Farouki 1981). This increase in thermal conductivity could result in moist soils experiencing higher temperatures than dry soils due to incoming solar radiation. However, soil moisture can also reduce soil temperature through evaporative cooling (Zhang *et al.* 2001). The presence of vegetation can reduce both direct solar radiation and evaporative cooling and buffer changes in soil temperature (Wang *et al.* 2009). In addition to the moderating effects of vegetation on soil temperature, experimental studies have found that increased soil

temperatures result in increased plant productivity (e.g., Hartley *et al.* 1999, Brooker and van der Wal 2003, Natali *et al.* 2012). Thus increases in soil temperature may be reinforced by increased vegetation cover that moderates soil temperatures in a direction favorable for plant growth.

Most nutrients in tundra environments are locked away in organic matter in the soil due to low soil temperatures and soil moisture causing slow decomposition and mineralization (e.g., Shaver *et al.* 1992, Jonasson *et al.* 1996, and 1999a). Tundra environments are not the only ones to experience high organic matter nutrient levels; many high-latitude environments, including sub-arctic and boreal, experience low decomposition due to low soil temperatures and sub-optimal soil moisture, including high or low moisture (Robinson 2002). Consequently these cold environments tend to have lower available nutrient levels than more temperate environments (e.g., Sowden *et al.* 1977, Nadelhoffer *et al.* 1992, Robinson 2002). Nitrogen is one of the most limiting nutrients for plant growth in arctic and alpine tundra (e.g., Shaver and Chapin 1980, Nadelhoffer *et al.* 1992, Atkin 1996). This nitrogen limitation is due to slow microbial release of plant available forms of nitrogen, both organic monomers and inorganic nitrogen (Schimel and Bennett 2004). Rates of soil nitrogen turnover, the transformation of one form of nitrogen to another, are affected by soil temperature, as well as by many of the same factors that affect soil temperature including soil moisture, snow cover, and vegetative cover (e.g., Jonasson *et al.* 1999a, Wu *et al.* 2006, Currie *et al.* 2010).

Increased soil temperatures have been associated with increased net nitrogen mineralization across arctic sites (e.g., Hartley *et al.* 1999, Rustad *et al.* 2001, Aerts *et al.* 2006). However, low levels of soil moisture may inhibit microbial activity, while very high soil moisture

levels have the same effect due to anaerobic conditions (Nadelhoffer *et al.* 1992, Prado and Airoldi 1999). Nitrogen mineralization is also increased by snow cover due to increased winter soil temperatures and the availability of unfrozen water (Borner *et al.* 2008), while during snow melt events nitrogen and moisture are released to the soil (Buckeridge and Grogan 2010). Alternatively, increased snow cover can decrease the length of the growing season by later dates of snow melt and thus initiation of vegetative growth (Larsen *et al.* 2007).

The objective of this study was to determine the existing relationships between soil temperature, nitrogen availability, soil moisture, snow depth, and plant productivity across an alpine vegetation gradient. Exploration of these patterns will lend insight into how future alterations to these environmental factors, due to climate change, might alter plant productivity on the landscape. To investigate these relationships I measured soil temperature, soil nitrogen, snow cover, soil moisture, and plant productivity in a series of plots located along a natural vegetation gradient in alpine tundra near Whitehorse, Yukon.

Based on theory and observations that plant growth in arctic and alpine tundra is most limited by nitrogen availability, I hypothesized that soil nitrogen would be the most important determinant of plant productivity, with soil temperature and moisture playing a secondary role by affecting nitrogen levels. If soil nitrogen was the environmental factor with the greatest influence on plant productivity and nitrogen was limiting, then the strongest correlation should occur between soil nitrogen and plant productivity. Additionally, if mean soil temperature was the most important moderating variable on soil nitrogen, then I should find a strong positive correlation between soil temperature and soil nitrogen. The patterns found along a spatial environmental gradient cannot be assumed to be the same patterns as would occur across time

(Dunne *et al.* 2004). Thus, determining the patterns present on the landscape, in conjunction with responses to environmental manipulation, can provide information about how a system works across both space and time. This study aims to provide further information regarding how various soil properties relate to plant productivity in northern environments, as well as to provide the relationships present along a natural gradient to integrate with an experimental soil warming and fertilization study occurring at the same site.

2.2 METHODS

2.2.1 Study Area

The study area (N 60°33'45.0", W 135°07'57.3", 1551 m asl) is located within the Wolf Creek drainage basin approximately 19 km from the city of Whitehorse, Yukon. Plots were located along toposequences that extended from an alpine ridge to a valley or hill slope approximately 40 m lower in elevation, and encompassing a range of slopes from 0° to 30°. The study area falls within the discontinuous/sporadic permafrost zone (Brown *et al.* 2001). The soil is classified as Orthic Eutric Brunisols; the underlying geography of the study site is mainly sedimentary in nature and is overlain by gravelly till with depths ranging up to 2 m (Janowicz 1999). The surface topography consists of shallow hummock-hollows, and cryoturbation occurs in the form of frost boils (areas lacking vegetation where seasonal freezing and thawing cycles result in areas with exposed mineral soil; Ping *et al.* 2003). This area experiences a sub-arctic climate, characterized by low relative humidity, low precipitation (300-400 mm annually with approximately 50% falling as rain), and large annual temperature variations with cool summers (mean monthly temperatures 5°C to 15°C) and cold winters (mean monthly temperatures -10°C to -20°C; Wahl *et al.* 1987, Janowicz 1999).

The study area is located within the Boreal Cordillera ecozone in the Yukon Southern Lakes ecoregion (Smith *et al.* 2004). The dominant tundra vegetation in this area includes erect shrubs such as *Betula glandulosa* Michx. (resin birch), *Cassiope tetragona* (L.) D. Don (white arctic mountain heather), *Salix glauca* L. (grayleaf willow); and prostrate shrubs such as *Dryas octopetala* L. (eightpetal mountain avens), *Salix arctica* Pall. (arctic willow), *Salix reticulata* L. (netleaf willow), *Vaccinium vitis-idaea* L. (lingonberry). Other dominant species include forbs such as *Lupinus arcticus* S. Watson (arctic lupine), *Polygonum viviparum* L. (syn. *Bistorta vivipara* (L.) Delarbre) (alpine bistort), *Pedicularis lanata* Cham. & Schltdl. (woolly lousewort), *Saxifraga tricuspidata* Rottb. (three toothed saxifrage); graminoids such as *Carex microchaeta* T. Holm (smallawned sedge), *Poa arctica* R. Br. (arctic bluegrass); as well as lichens such as *Cetraria* species and mosses such as *Polytrichum* species. Taxonomic nomenclature follows the Integrated Taxonomic Information System online database (ITIS 2012).

2.2.2 Study Design

Plots were established in July 2010 based on a stratified random design. Two hills were selected that exhibited the presence of all five target vegetation types: wind-swept ridge (wind tolerant plants, low canopy), low-shrub tundra (prostrate shrubs, lichen and forbs), tall-shrub tundra (dominated by erect growing shrubs >10 cm), late-lying snow bed (short season species), and frost boils (very little plant growth on disturbed mineral soil). Two sampling areas were placed on each hill, one north facing and one south facing, for a total of four sampling areas. Plots were spread out at different elevations on both north and south facing slopes in attempt to encompass the range of microclimate conditions experienced in this landscape. For example, plots may experience differences in incoming solar radiation with different aspects (e.g.,

McCune and Keon 2002, Allen et al. 2006, Wundram et al. 2010) or soil moisture with different slopes (e.g., Western *et al.* 1999, Janowicz *et al.* 2004, Penna *et al.* 2009). Plots were randomly assigned within each sampling area depending on the vegetation type. For the windswept ridge, low shrub, and tall shrub vegetation types, a central point for the area containing those vegetation types was selected and then plots were placed according to random directions and distances from that point. Five digit random numbers were used to determine direction and distance for each plot, the first three digits established compass direction and the last two established distance. Frost boils and late-lying snow beds were less common on the landscape, so they were identified, numbered and then three were selected at random. An exception was sampling area 3, where frost boils were so numerous they were selected using the central point method. Three replicate plots within each of the five vegetation types were randomly selected at each area for a total of 15 plots per sampling area and 60 plots in total (see Appendix A, Table A.1). Each 1 m^2 plot was oriented north-south so that it was square with the ridge top.

2.2.3 Field Measurements

Location, elevation, and slope data were collected in July 2010 when plots were established. Soil temperature was monitored using an iButton temperature datalogger (Maxim Integrated Products Inc, Sunnyvale, CA) inserted 5 cm below the soil surface in the centre of each plot. Temperature was measured at 255 minute intervals (4.25 hours, the maximum collection interval to obtain a long time record) over one year from 9 August 2010 to 6 August 2011. Total nitrogen was determined from soil samples collected 21 and 22June during the 2011 field season. Each soil sample was dug with a trowel to approximately 10 cm x 10 cm and 6 - 10 cm depth, depending on the presence of large rocks. To assess the spatial patterns in soil moisture,

small soil samples, 5 cm x 5 cm and 6 - 8 cm depth, were collected to determine gravimetric soil moisture. These were collected from the edges of the plots to avoid disturbing the vegetation before plant productivity measurements. Soil samples used for gravimetric soil moisture were restricted to those that were collected from all 60 plots within a single day to avoid differences in soil moisture due to time. Samples were also restricted to periods without rainfall, with at least two days between rainfall and sampling. Due to time constraints in the field only two dates were sampled, 30 June and 17 July 2011. Undecomposed litter on top of the soil samples and rocks over 1 cm diameter were removed during sample collection.

To assess both the spatial and temporal variability in snow cover, two different measurements of snow depth were taken. Twelve plots were randomly selected for continuous snow depth monitoring, from Sept 2010 until snow melt in 2011. The plots belonged to the following vegetation types: two wind-swept ridge plots, three low-shrub tundra plots, three tall-shrub tundra plots, three late-lying snow bed plots, and one frost boil plot. Snow depth monitors (Lewkowicz 2008) were placed at the edge of the plot that was closest to the ridge. The snow depth monitors were 1 m tall stakes with temperature dataloggers, iButtons, positioned at 10 cm intervals along the length of the stake. The dataloggers monitored temperature every four hours. Snow depth was determined by assessing the temperature profiles recorded on adjacent dataloggers. Dataloggers below the snow surface experience warmer temperatures due to the insulating qualities of snow, and as such show a noticeable alteration to the diurnal temperature fluctuation as compared to that experienced by exposed dataloggers (Lewkowicz 2008). Snow depth was considered to fall between the placement heights of the two highest adjacent dataloggers which showed a temperature difference of at

least 1°C and reduced diurnal temperature fluctuations. For example, when dataloggers placed at 10 cm and 20 cm show differences, snow depth was considered to be 15 cm. If there was also a difference between 20 cm and 30 cm dataloggers the depth was considered to be 25 cm. Manual snow depth measurements were also taken on 19 February 2011 with a 120 cm calibrated steel probe. Only 43 plots were measured due to poor weather conditions and low visibility, six of which also had snow depth monitors present.

The plant productivity measures were taken on both the whole plot level and at the level of plant functional groups. A LI-2000 meter (LI-COR, Lincoln, NE) was used to determine leaf area index (LAI), the ratio of one sided leaf surface to ground area, which is tightly linked with biomass production (van Wijk and Williams 2005). Four LAI measurements were taken within each plot, averaged and compared against a single reference measurement taken above the canopy. The LI-2000 probe can disturb the leaves in shorter canopies and often cannot be inserted beneath the leaves. Thus the LAI method is limited for accurately determining biomass for canopies of less than 3 cm (LI-COR 1992). Plant productivity was also measured using the point-intercept method, visual percent cover, and canopy height. The point-intercept method used here is a modification of the Levy and Madden (1933) method, and is similar to that proposed by Stanton (1960) with 100 points 10 cm apart in a 1 m^2 grid. At every point a long pin was lowered and each intersection of the pin with current year vegetation, called a 'hit', was recorded by functional group: deciduous shrubs, evergreen shrubs, graminoids, and forbs. These functional groups were similar to those proposed by Epstein *et al.* (2001), except grasses, sedges, and rushes were grouped together into graminoids. Visual percent cover was recorded to the closest 1% using the point-intercept grid to aid in calibrating estimates. Categories

included the four functional groups, litter/previous year vegetation, lichen/moss, rock, and bare soil. Green photosynthetic tissue on evergreen shrubs was considered to be current year productivity because of the difficulty in separating current year from past growth in evergreen shrubs. Canopy height, measured from the top of the lichen surface or bare soil to the top of the tallest intersecting plant, was averaged from five measurements within each plot.

2.2.4 Laboratory Methods

All soil samples were weighed upon collection, oven dried at 105 °C for 48 hrs, re-weighed to get the dry weight, then passed through a 2 mm sieve to remove rocks and homogenize the sample. Gravimetric soil moisture as grams of water per gram of dry soil ($g\ g^{-1}$) was calculated as wet weight minus dry weight, divided by dry weight. A 2 to 6 g sub-sample of soil was taken to be further homogenized and reduced to a fine powder using a ball mill for 24 hrs and then processed for total nitrogen. These sub-samples were analyzed concurrently for total carbon and total nitrogen using a TruMac CN (LECO, St. Joseph, MI) giving total nitrogen as a percent of sample dry weight. Total nitrogen was converted into milligrams nitrogen per kilogram of dry soil ($mg\ N\ kg^{-1}$) before further analysis.

2.2.5 Statistical Analyses

All statistical analyses were performed in R (R Development Core Team 2011) and an α-level of 0.05 was used to assess statistical significance. Prior to analyses, data checking and unit conversions were performed. The predicted heat load for each plot was calculated using latitude, aspect, and slope (McCune and Keon 2002). The aspect of each plot was estimated using ArcGIS (Version 9.3, Environmental Systems Research Institute, Redlands, CA) to extract the information from a digital elevation model (DEM). The DEM used was the 1:50,000 scale

map of 105D11 in the National Topographic System (NTS) using the NAD83 horizontal reference datum with elevations in meters relative to mean sea level (GeoBase – Canadian Digital Elevation Data).

Temperature data were first checked for errors and missing values. One datalogger had a technical failure, recording no data, and four other plots were removed from further analyses because they had been unburied at some point during the recording time, likely due to ground squirrel activity, and thus were recording surface air temperatures. Mean soil temperature was calculated from all soil temperature data collected, from 9 August 2010 to 6 August 2011. The soil temperature coefficient of variation was also calculated to provide a measure of the temperature variability experienced in each plot. Before this calculation, the raw soil temperature data was converted from degrees Celsius (interval scale) to Kelvin (ratio scale), to get rid of negative values. I examined seasonal soil temperature measures and found that all seasonal soil temperature coefficient of variation measures were significantly correlated with the annual coefficient of variation measure, while only mean summer soil temperature differed from mean soil temperature based on a full year's data. Due to the similarities between the seasonally and annually calculated soil temperature measurements all analyses involving soil temperatures reported here used the values based on the full year's data. Further examination of seasonal mean soil temperatures were used to help describe patterns between productivity and soil temperature.

Differences in productivity measurements, environmental variables, and predicted heat load between vegetation types were assessed with one-way ANOVA's (Crawley 2007). The *aov* function in R fits ANOVA's using a linear model for both unbalanced and balanced designs (R

Development Core Team 2011), so the unbalanced nature of some of these one-way ANOVA's will not affect the model estimates. To determine the differences between groups Tukey HSD post-hoc tests were selected for balanced ANOVA's (Crawley 2007), while a modified version for unequal variances and unbalanced designs (Herberich *et al.* 2010) was used for unbalanced ANOVA's.

A rank correlation of the six plots with both snow measurements was used to determine if manual snow depths measured at one point in time could reasonably represent average snow depth through the winter. A rank correlation was chosen because the relative distributions of snow depths were of greater importance than the actual values. The manual snow depths were ranked from lowest to highest and plotted against the rank of the snow depths at four times throughout the snow covered season; once each in October, December, February, and April. Due to the coarse nature of the snow depth monitor measurements, depths estimated to 0, 5, 15, 25 cm, etc., several plots showed the same snow depth at the same time period. To break the ties in rank that this produced, the plot that had greatest snow depth during that month or had the longest period of continuous snow cover over the month was assigned the higher rank. Spearman's rank correlation coefficient, rho, was calculated for each combination of measurements. Spearman's rho is calculated the same way as Pearson's r, with values between -1.0 and 1.0. The value indicates the strength of the relationship, and the sign indicates if it is positive or negative (Ludwig and Reynolds 1988).

A synthetic variable to describe plant productivity was derived from principle component analysis (PCA) using the package 'labdsv' (Roberts 2010). The PCA contained information from all 60 plots on 4 productivity variables: total vascular hits, percent cover of vascular plants, LAI,

and canopy height measurements. PCA reduces the dimensionality of a data set by creating synthetic variables that describe the covariation of the data (McCune and Grace 2002). These synthetic variables, the principle components, are orthogonal, and are arranged in order of decreasing variance explained by each component. The plant productivity synthetic variable was obtained from the first principle component, which contained the highest amount of variance in the data set (McCune and Grace 2002)..

Linear correlation analyses were used to assess the relationships between environmental and productivity measures (Crawley 2007). The strength of each relationship was assessed using Pearson's product-moment correlation coefficients, r, between -1.0 and 1.0, where an increasing value indicates a stronger relationship, and the sign indicates if it is a positive or negative relationship (Crawley 2007). To assess the goodness of fit of linear correlations using raw data vs. log transformed variables, diagnostic plots were viewed. These included a plot of the standardized residuals and fitted values from the model, as well as a Q-Q plot of the standardized residuals against theoretical quantiles (Crawley 2007). Diagnostics using untransformed soil moisture data showed a pattern of increasing variance with the mean, or heteroscedasticity, which was improved following log transformation. Soil moisture was log transformed for all analyses to improve normality, and all other variables were untransformed. Both June and July soil moisture measurements showed similar relationships with all other variables, but the June measurement had stronger correlations than the July measurement. All analyses involving soil moisture reported here used the 30 June measurement.

2.3 RESULTS

2.3.1 Vegetation Types and Environmental Gradients

Productivity in the plots showed a great deal of variation, both across the landscape and within vegetation types. The number of hits of current year vascular tissue ranged from 16 to 440, leaf area index (LAI) ranged from 0.02 to 3.09, canopy heights ranged from 0.2 to 42.8 cm, and total vascular percent cover ranged from 9.1 to 85%. Tall shrubs showed both the highest levels and the greatest variation in total hits, LAI, and canopy height (Fig 2.1a to c), while the other four vegetation types, wind-swept ridge, low-shrub tundra, late-lying snow bed, and frost boils, had greater variation in total vascular percent cover (Fig 2.1d). The different productivity measurements showed similar patterns between vegetation types, with tall shrubs consistently having the highest values. Late-lying snow beds grouped out as having the second highest canopy height and LAI, while their measures of total vascular hits and vascular percent cover were similar to the other vegetation types.

The plant productivity index used in the correlation analyses was created from a PCA of total vascular hits, LAI, canopy height, and total vascular percent cover (60 plots x 4 variables). The first principle component, PCA Axis 1, accounted for 86% of the variance in the productivity data, and was strongly correlated with the four productivity measures (Fig 2.2a to d). PCA Axis 1 was used as an index of productivity in the plots. The points at the higher end of the productivity index are the tall shrub plots, while all other vegetation types are overlapping at lower levels of productivity. The productivity index showed similar patterns of variation between habitat types as those exhibited by the raw productivity measurements (Fig 2.1 & 2.3). Productivity in tall shrubs was estimated to be at least double the level apparent in the other

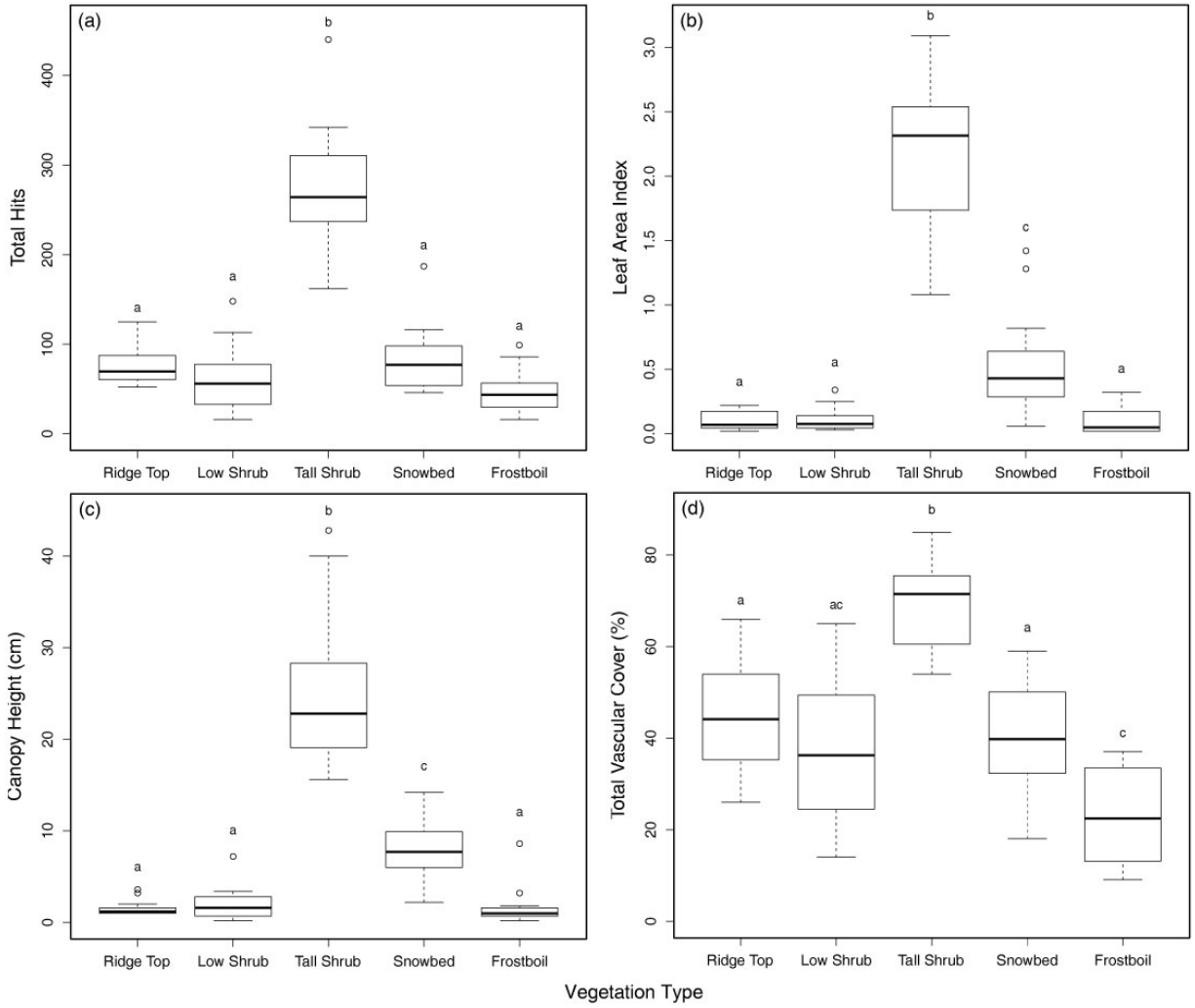

Figure 2.1: Estimates of plant productivity across five vegetation types, using four different metrics: (a) total number of point intersections with vascular plants, (b) leaf area index, (c) canopy height, and (d) total vascular percent cover (n = 12 per vegetation type). Vegetation types labeled with different letters were significantly different in a Tukey multiple comparison test following a significant single-factor analysis of variance. The centre line represents the median, the boxes contain the 25^{th}-75^{th} quartiles of the data, and the whiskers extends to the most extreme data point that is less than 1.5 times the interquartile range with extreme values beyond the whiskers shown as hollow circles.

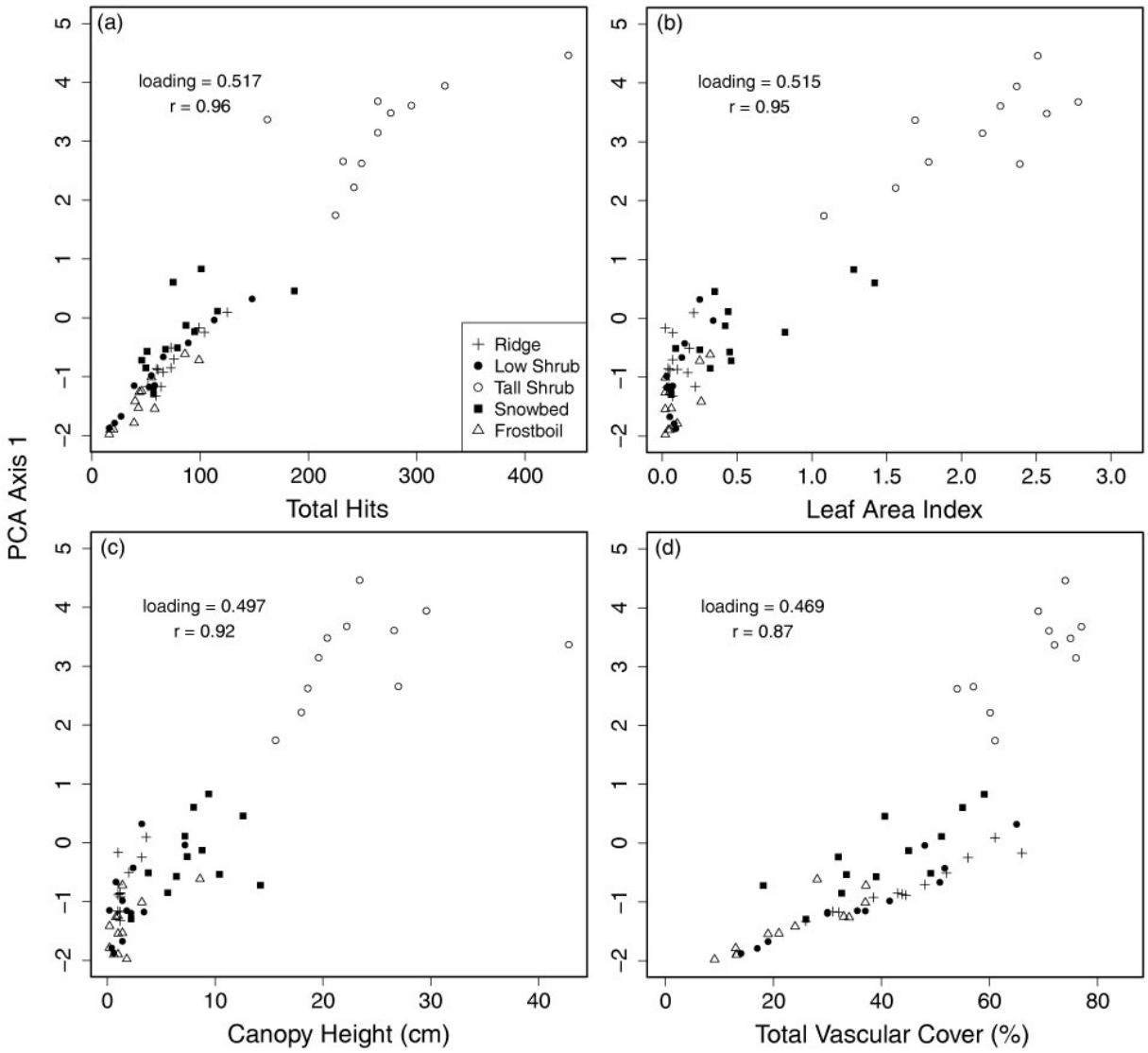

Figure 2.2: Scatter plots of PCA Axis 1, used for the plant productivity index, with the four productivity measurements used for the PCA; (a) total vascular hits, (b) leaf area index, (c) canopy height, and (d) total vascular cover. The PCA was run on data from 60 plots on the 4 productivity variables shown here. The loading indicates the factor loading associated with each measurement and Axis 1, r is the Pearson Product correlation coefficient, and each plot is represented by a symbol corresponding to the vegetation type (n = 12 per vegetation type).

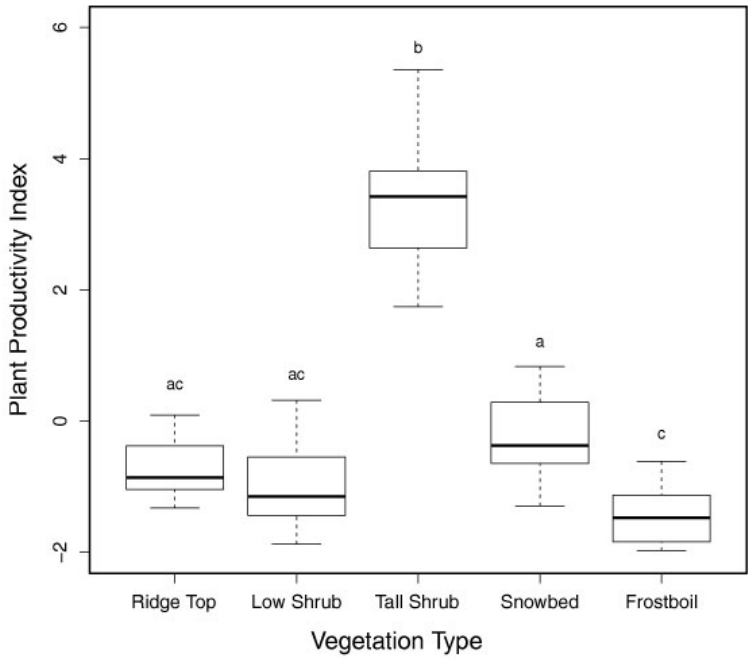

Figure 2.3: Plant productivity index as a function of vegetation type (n = 12 per vegetation type). The PCA was run on data from 60 plots on 4 productivity variables. Vegetation types labeled with different letters were significantly different in a Tukey multiple comparison test following a significant single-factor analysis of variance. The centre line represents the median, the boxes contain the 25^{th}-75^{th} quartiles of the data, and the whiskers extends to the most extreme data point that is less than 1.5 times the interquartile range with extreme values beyond the whiskers shown as hollow circles.

vegetation types, while frost boil plots had most of the lowest estimates of productivity. Ridge top and frost boil plots had the least variability in productivity.

The abundance of deciduous shrubs (Fig 2.4a), evergreen shrubs (Fig 2.4b), forbs (Fig 2.4c), and graminoids (Fig 2.4d) also varied between the vegetation types, although all functional groups were found in each vegetation type. Tall shrub habitats were dominated by deciduous shrubs, with much higher abundances than in any other vegetation type. The second most abundant functional group was graminoids, which had a high number of hits and a relatively low percent cover, probably due to being present mostly below the canopy of deciduous shrubs. Evergreen shrubs and forbs were present in tall shrub habitats, but at a lower abundance than in other vegetation types. Late-lying snow beds were dominated by evergreen shrubs, followed by approximately equal amounts of graminoids, deciduous shrubs, and forbs. While forbs were the last in terms of dominance in snow bed plots, forbs were more common in snow bed plots than any other vegetation type. Low shrub habitats were equally dominated by evergreen and deciduous shrubs. Wind-swept ridge plots were dominated by evergreen shrubs while frost boils were dominated by deciduous shrubs. There was very little vegetation within the frost boils themselves, so the relatively high abundance of deciduous shrubs in frost boil habitats was mostly due to the vegetation within the sampling plots that were from the margins of the frost boils.

Differences between habitat types also occurred in their non-vascular cover: rocks (Fig 2.5a), bare soil (Fig 2.5b), and lichen and moss (Fig 2.5c). Frost boils had the highest cover of rocks and bare soil due to cryoturbation exposing the mineral soil. Ridge top habitats also had more rock cover than other vegetation types, likely because of the wind scouring the ridges

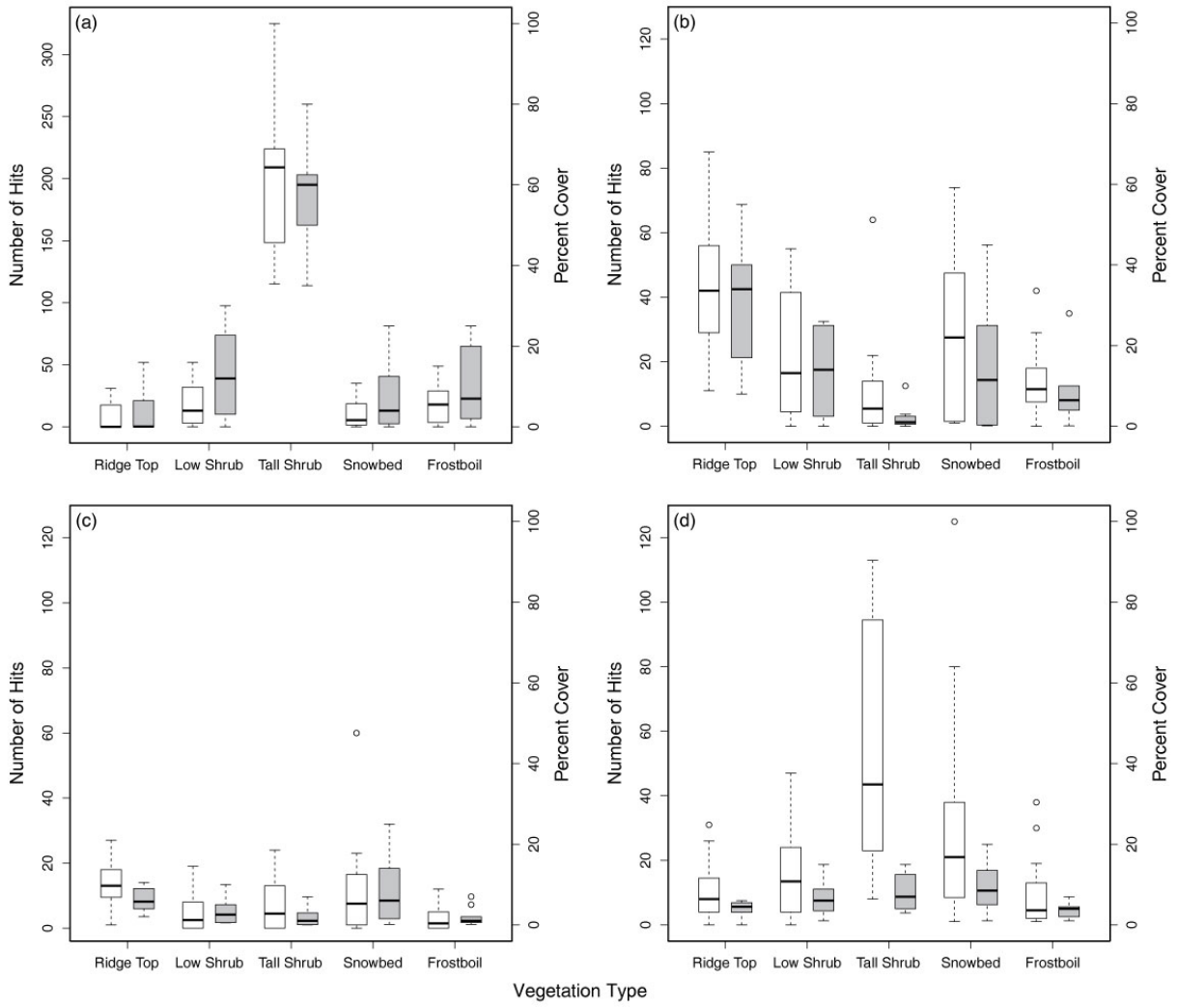

Figure 2.4: Abundance of functional groups, (a) deciduous shrubs, (b) evergreen shrubs, (c) forbs, and (d) graminoids, in each vegetation type (n = 12 per vegetation type). Abundance was measured by the number of point intercept hits and percent cover (white and gray boxes, respectively). Note that the scale of the number of point intercept hits in the deciduous shrub figure differs from the other figures. The centre line represents the median, the boxes contain the 25^{th}-75^{th} quartiles of the data, and the whiskers extends to the most extreme data point that is less than 1.5 times the interquartile range with extreme values beyond the whiskers shown as hollow circles.

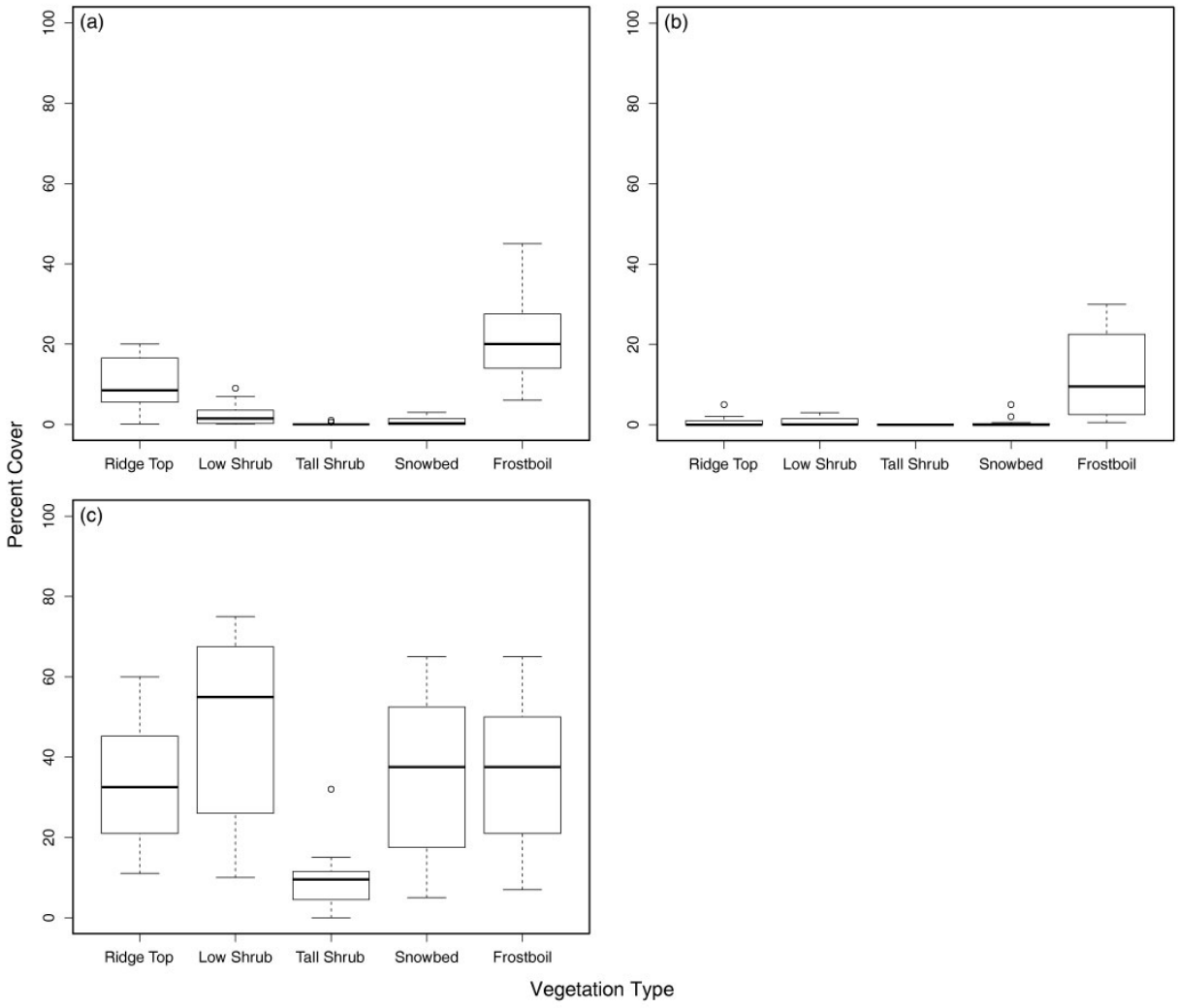

Figure 2.5: Percent cover of (a) rock, (b) bare soil, and (c) lichen and moss, in each vegetation type (n = 12 per vegetation type). The centre line represents the median, the boxes contain the 25^{th}-75^{th} quartiles of the data, and the whiskers extends to the most extreme data point that is less than 1.5 times the interquartile range with extreme values beyond the whiskers shown as hollow circles.

with sufficient force to impede colonization. Lichen and moss cover was similar between all habitat types except tall shrubs. The tall shrub habitats did have similar lichen and moss growth on the soil surface as compared to other vegetation types (personal observation), but the low percent cover is likely due to being covered by the canopy of deciduous shrubs.

Environmental factors also varied across the landscape and within vegetation types. Total nitrogen ranged from 611 to 24200 mg N kg^{-1}, with a median of 8667 mg N kg^{-1}, and was highly variable within vegetation types (Fig 2.6a). However, frost boils were less variable and had significantly lower nitrogen than the other vegetation types. Total nitrogen and total carbon were strongly correlated (Fig 2.7), which indicates that this variability in soil nitrogen content could be due to the proportion of organic soil in the samples. Soil moisture ranged from 0.097 to 2.296 g g^{-1}, with the lowest values and least variability found in wind-swept ridges and frost boil habitats and the highest values and most variability in late-lying snow beds (Fig 2.6b).

Mean soil temperature ranged from -3.4 to 1.1 °C while the coefficient of variation of soil temperature ranged from 0.008 to 0.353. Mean soil temperature and soil temperature coefficient of variation were inversely correlated, with higher coefficient of variations associated with lower mean temperatures (Table 2.1; Fig 2.6c, d & 2.8). Late-lying snow bed and tall shrub plots had the lowest coefficient of variation of the vegetation types, but the highest mean soil temperatures were found in the snow bed and frost boil plots. However, frost boils also had the greatest variation in soil temperatures due to the lack of the moderating effect of vegetation on their exposed soil surface. Variation within a habitat type was higher in mean soil temperatures than coefficient of variations. This indicates that while the actual temperatures might differ to a high degree between plots within the same vegetation type, the

Table 2.1: Correlation matrix showing a summary of bivariate correlations between the plant productivity index and environmental measurements. Soil moisture was log-transformed prior to analyses to improve normality. Significant p-values are in bold font.

			Plant Productivity Index			Soil Temperature			
	Measurement		All Habitat Types	Without Tall Shrubs	Tall Shrubs Only	Mean Temperature	Coefficient of Variation	Total Nitrogen	Soil Moisture
Soil Temperature	Mean Temperature	r	0.09	0.34	0.70				
		P	0.526	**0.027**	**0.012**				
	Coefficient of Variation	r	-0.39	-0.29	-0.38	-0.71			
		P	**0.003**	0.060	0.226	**<0.001**			
	Total Nitrogen	r	0.43	0.60	-0.06	0.01	-0.22		
		P	**<0.001**	**<0.001**	0.861	0.967	0.105		
	Soil Moisture	r	0.38	0.48	0.31	0.34	-0.53	0.66	
		P	**0.003**	**<0.001**	0.319	**0.013**	**<0.001**	**<0.001**	
	Snow Depth	r	0.16	-0.34	0.05	0.45	-0.63	-0.16	0.16
		P	0.317	0.055	0.888	**0.004**	**<0.001**	0.319	0.298

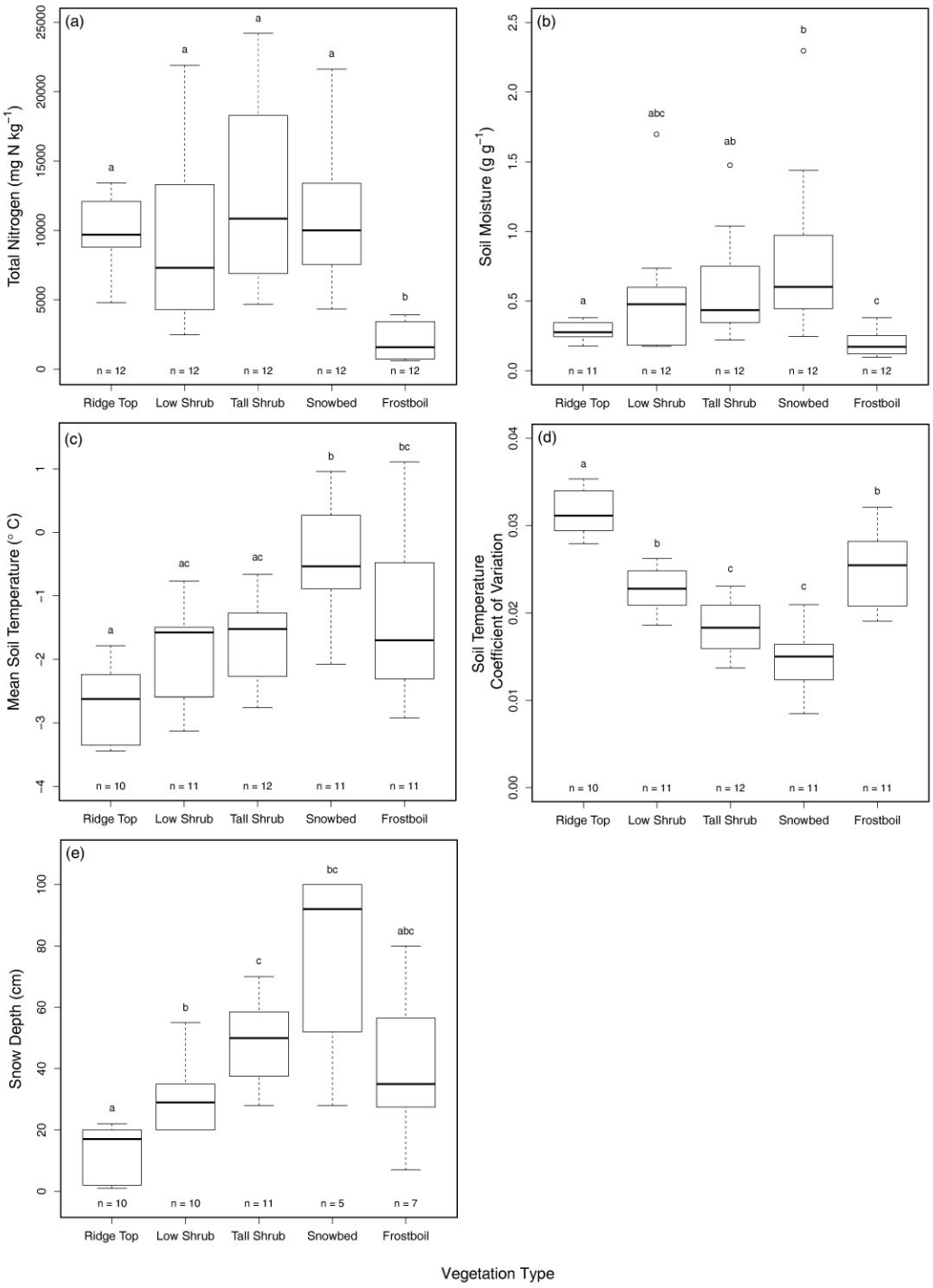

Figure 2.6: Environmental measurements, (a) total nitrogen, (b) soil moisture, (c) mean soil temperature, (d) coefficient of variation of soil temperature, and (e) snow depth, as a function of vegetation type. Vegetation types labeled with different letters were significantly different in a Tukey multiple comparison test following a significant single-factor analysis of variance. The centre line represents the median, the boxes contain the 25th-75th quartiles of the data, and the whiskers extends to the most extreme data point that is less than 1.5 times the interquartile range with extreme values beyond the whiskers shown as hollow circles.

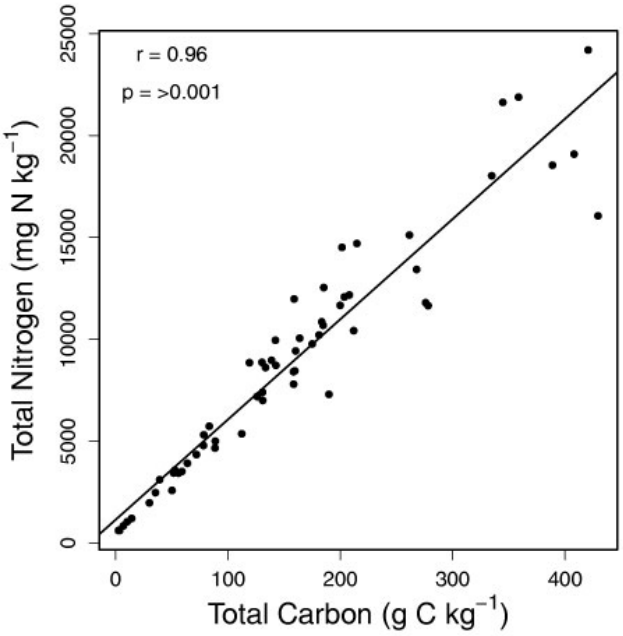

Figure 2.7: Bivariate relationship between soil sample contents of total nitrogen and total carbon (n = 60).

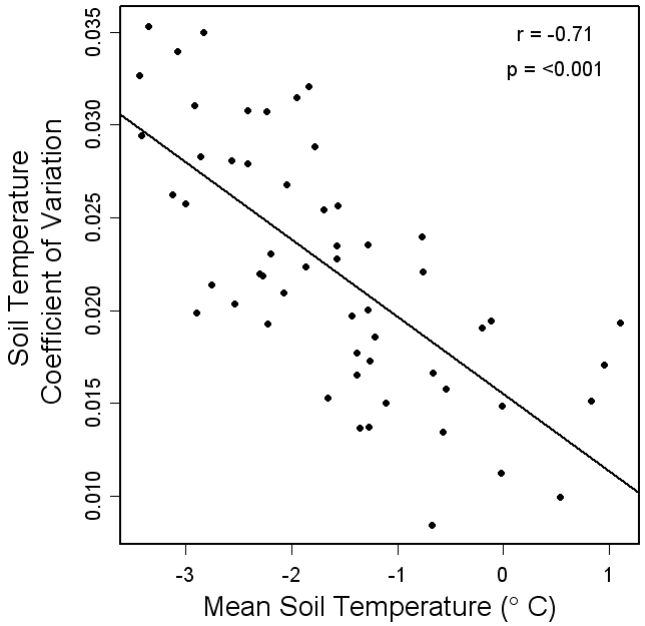

Figure 2.8: Bivariate relationship between the soil temperature coefficient of variation and mean soil temperature (n = 55).

change in soil temperature that a single plot experiences throughout the year is similar to the other plots within the same vegetation type. The variation in these soil temperature measurements indicate that the soil temperature gradient present at this site could not be fully predicted based on the vegetation types. Further assessment of the origin of the soil temperature gradient found that soil temperature was also poorly predicted by heat load, a calculation based on latitude, aspect, and slope, with a weak correlation with soil temperature coefficient of variation ($r = 0.27$) and no significant correlation with mean soil temperature, but that mean soil temperatures were higher on south-facing slopes (see Appendix B).

Snow depth ranged from 1 to 100 cm, and was quite variable within habitat types with no single vegetation type significantly different from all other vegetations types (Fig 2.6e). The greatest variation was present in the late-lying snow bed and frost boil plots, and they were also the plots with the lowest sample sizes ($n = 5$ and 7, respectively). The variation in frost boil habitats was due to their locations on the landscape. They were located much more evenly across the landscape than any other vegetation type, and thus were exposed to a wide variety of environments from wind-swept ridges to the sheltered edges of tall shrubs. The wind-swept ridge plots had much shallower snow depths than the other vegetated plots, which was due to both the locations of the plots being more exposed to scouring winds and the lower stature vegetation. As expected the greatest snow depths were found in the late-lying snow bed plots. However, the high amount of variation was most likely due to the placement of some snow bed plots near the edges of the snow bed depressions. The pattern of snow depths within vegetation types (Fig 2.6e) was very similar to that of mean temperatures (Fig 2.6c), and negatively correlated with the soil temperature coefficient of variation (Fig 2.6d). These strong

correlations between snow depth and soil temperature measurements within vegetation types are consistent with the influence that vegetation and snow cover have on soil temperature, examined further in the discussion section.

Examination of the different snow measurements indicated that the snow depth measurement used in these analyses, a single depth measurement from 19 February 2011, was significantly correlated to the continuously monitored snow depths (Fig 2.9), and as such was a good proxy for relative snow cover both spatially and temporally. The correlation coefficient for the October snow depths was quite high, but not significant due to the small number of samples (n = 6; Fig 2.9).

2.3.2 Environmental and Productivity Correlations

Several significant correlations appeared among the environmental variables analyzed in this study (Table 2.1). Snow cover was not correlated with soil moisture, but did show significant correlations with soil temperature measurements (Fig 2.10a & b). There was no significant relationship between soil temperature and soil nitrogen (Fig 2.11a & b). Soil moisture was related to both soil temperature and soil nitrogen, with a negative relationship with soil temperature coefficient of variation (Fig 2.12a), and positive relationships with mean soil temperature (Fig 2.12b) and total nitrogen (Fig 2.13).

Plant productivity showed significant correlations with all environmental variables excluding snow depth; however, the slope and strength of the relationships were dependent on the inclusion of tall shrubs (Table 2.1). The relationships of tall shrub plant productivity with all environmental variables were different as compared to the other vegetation types (Fig 2.14a to d). The tall shrubs consistently showed higher levels of productivity at similar levels of each

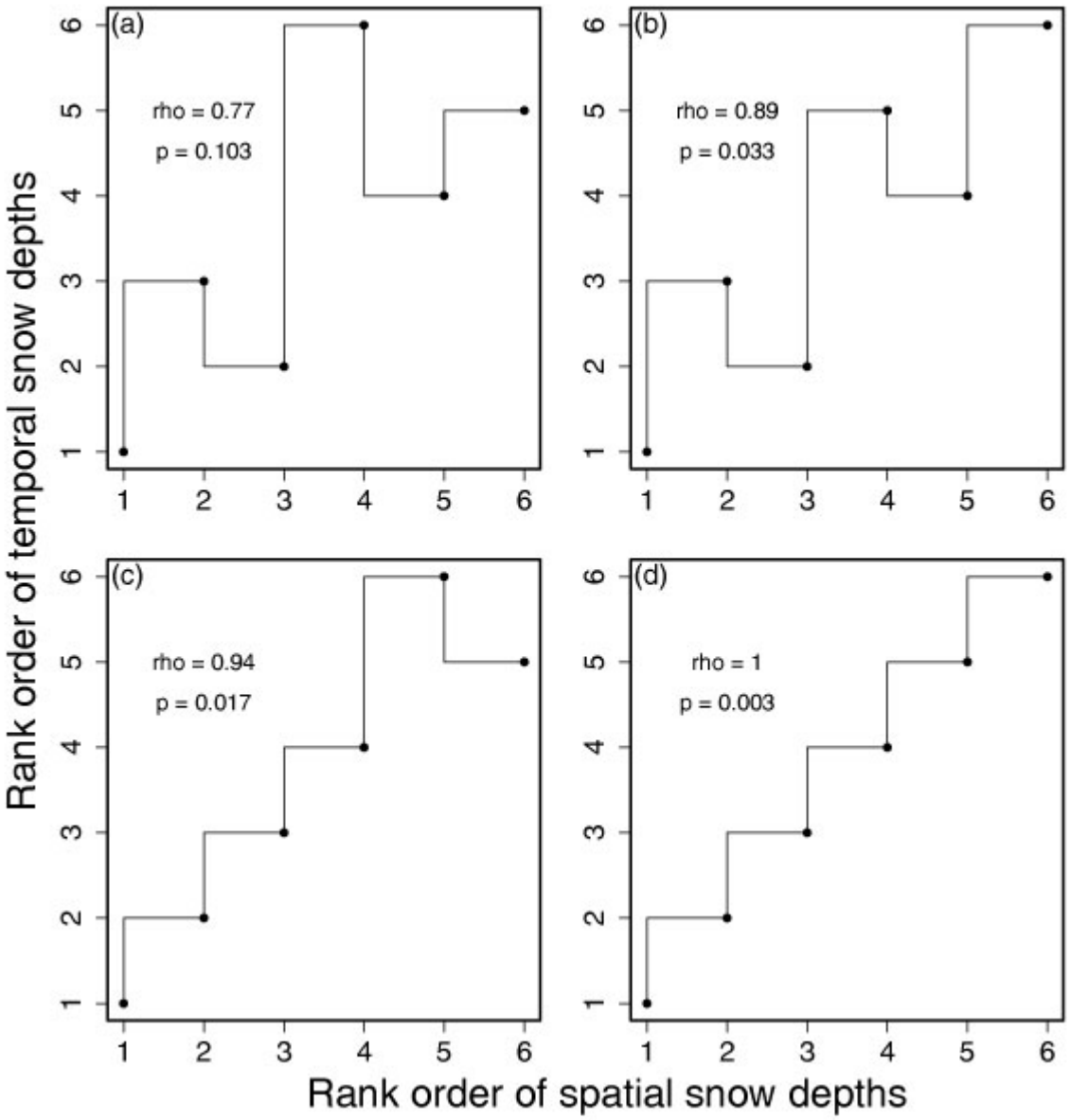

Figure 2.9: Relationship between snow depth measurements taken 19 February 2011 to capture spatial variability and those taken over time to capture temporal variability (n = 6). Snow depths are compared in (a) October, (b) December, (c) February, and (d) April. Plots are ranked from smallest to largest measurements. Spearman's correlation coefficient, rho, and associated p-values are indicated on each plot.

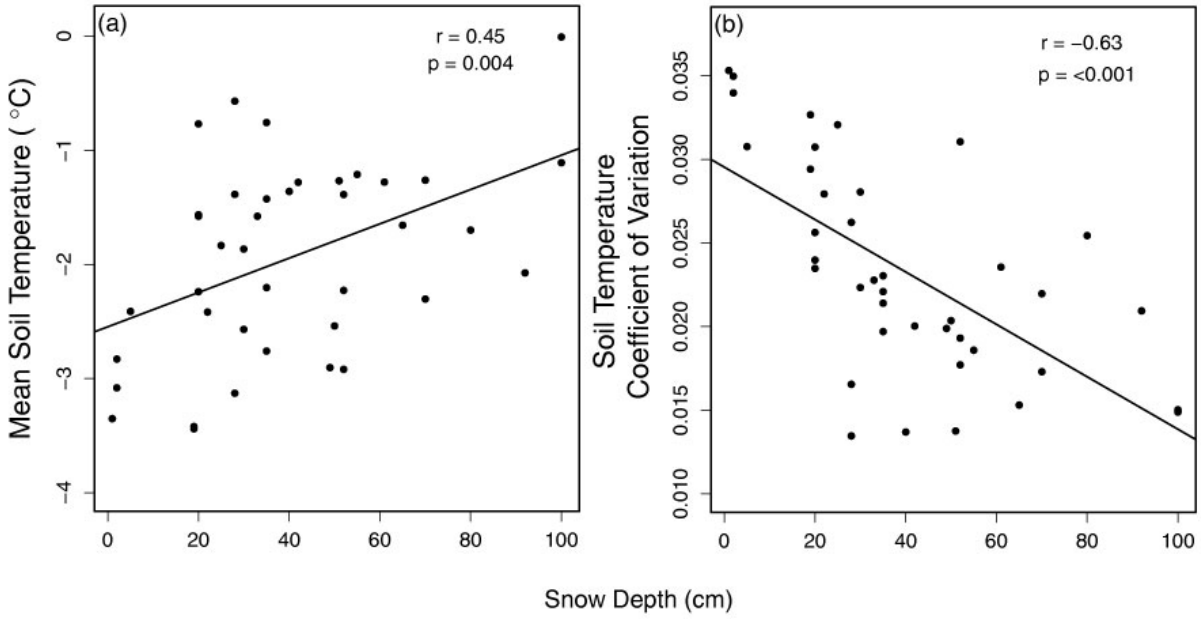

Figure 2.10: Bivariate relationships between soil temperature measurements, (a) mean temperature and (b) coefficient of variation, and snow depth (n = 39).

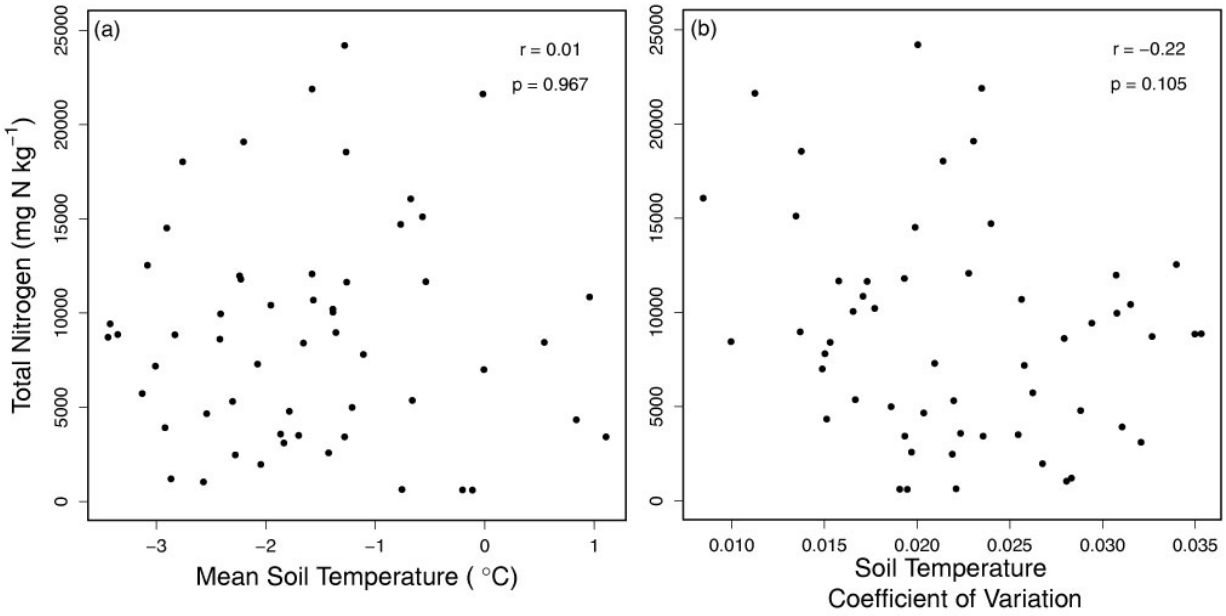

Figure 2.11: Bivariate relationships between total nitrogen and soil temperature measurements, (a) mean temperature and (b) coefficient of variation (n = 55).

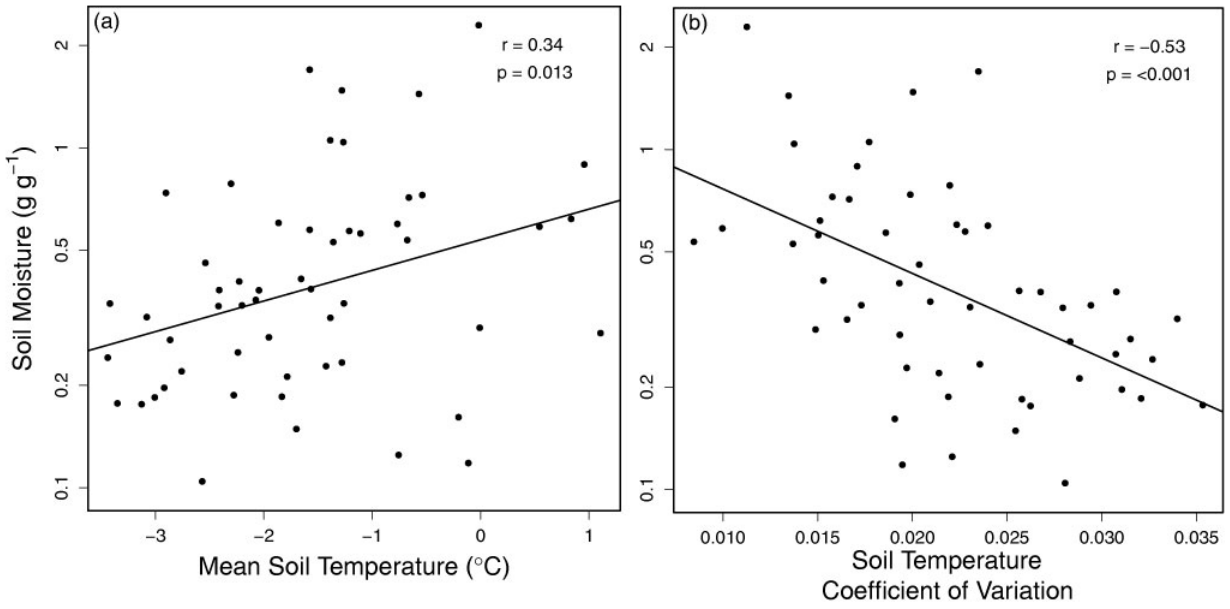

Figure 2.12: Bivariate relationships between soil moisture and soil temperature measurements, (a) mean temperature and (b) coefficient of variation (n = 54). Soil moisture is plotted on a $\log_{10}$ scale.

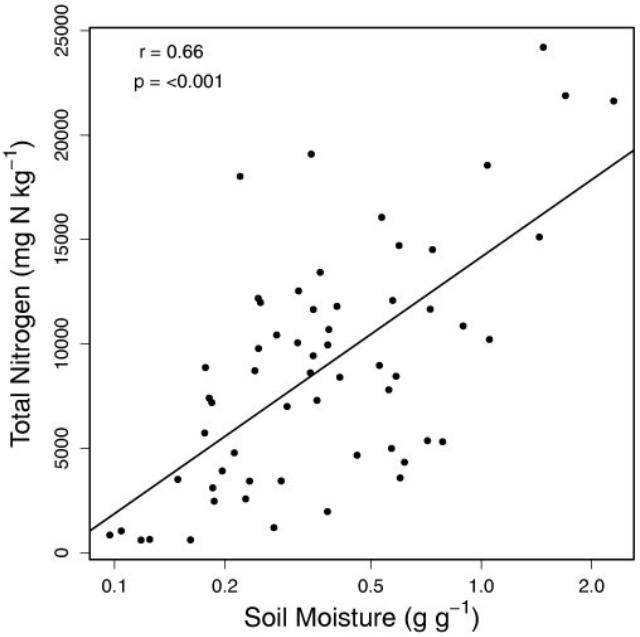

Figure 2.13: Bivariate relationship between total nitrogen and soil moisture (n = 59). Soil moisture is plotted on a $\log_{10}$ scale.

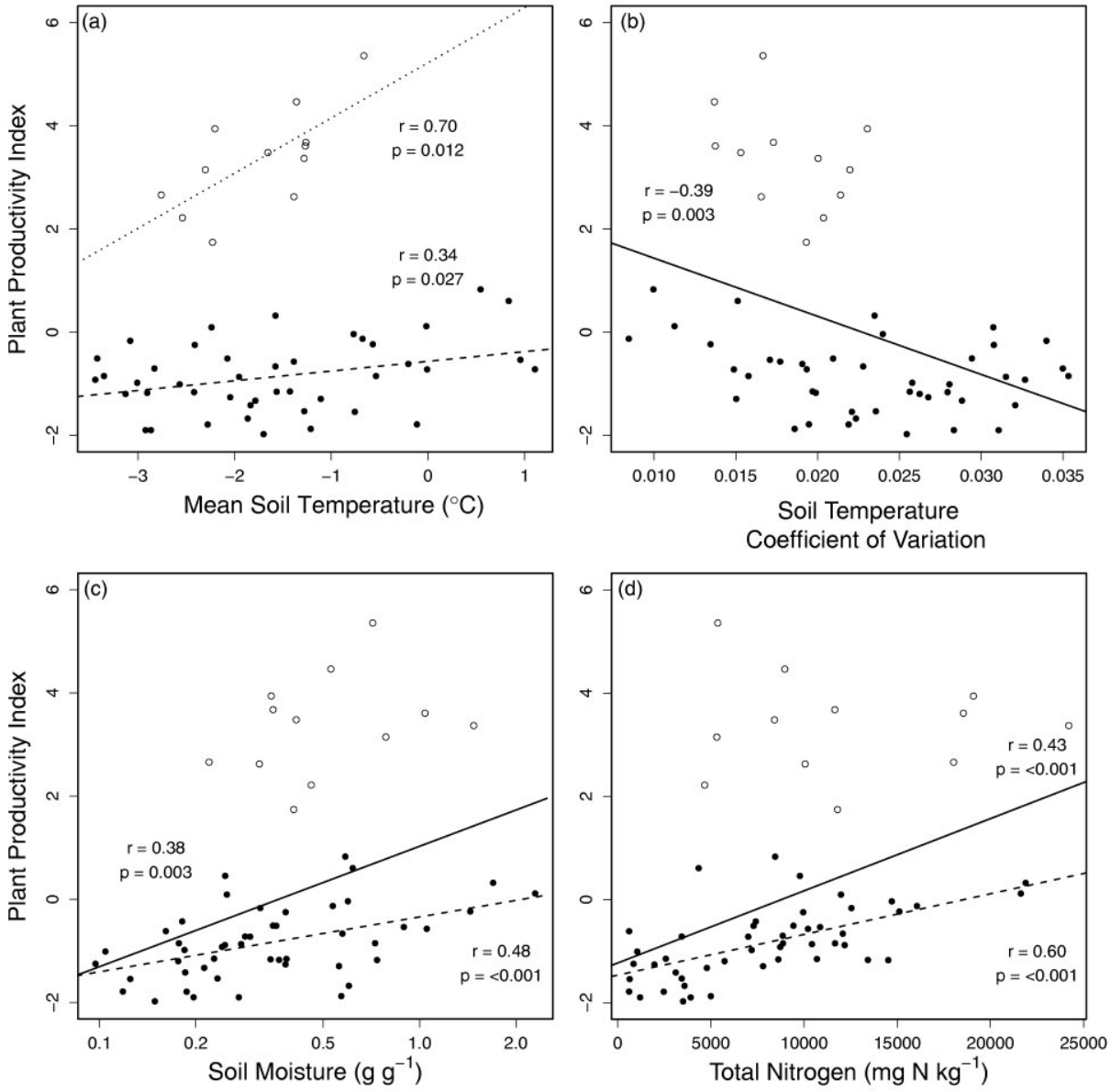

Figure 2.14: Bivariate relationships between plant productivity index and (a) mean soil temperature, (b) soil temperature coefficient of variation, (c) soil moisture, and (d) total nitrogen. The solid lines represent linear models including all points in the figure (n = 55, 55, 59, and 60 plots respectively), the dashed lines represent linear models fit only to filled circles, which excludes the tall shrubs (n = 43, 43, 47, and 48 plots respectively), and the dotted lines represent linear models fit only to tall shrubs, which are represented by open circles (n = 12 plots). Soil moisture is plotted on a $\log_{10}$ scale.

environmental variable as compared to every other vegetation type. This is consistent with the differences in vegetation type productivity measurements and environmental factors discussed above, where tall shrubs always had the highest productivity, regardless of the measurement (Fig 2.1a to d), but they did not stand out with different environmental conditions as compared to the other vegetation types (Fig 2.6a to e). With all vegetation types included in the analyses, the only significant correlations were with soil temperature coefficient of variation, soil moisture, and total nitrogen (Fig 2.14a, c, & d, respectively). Seasonal mean soil temperatures were analyzed separately for relationships with plant productivity. Mean summer temperature was negatively correlated with productivity only when all vegetation types were included in the analysis (Fig 2.15), all other seasonal mean soil temperatures gave similar results as those with mean soil temperature calculated with a full year's data. Removing the tall shrub plots from the analyses produced stronger correlations with all variables except soil temperature coefficient of variation, and resulted in a significant positive relationship with mean soil temperature (Table 2.1; Fig 2.14b). Regardless of what vegetation types were included in the analyses, total nitrogen and soil moisture showed the strongest correlations with plant productivity (Table 2.1). When tall shrubs were analyzed separately from the other vegetation types, only mean soil temperature showed a significant correlation with plant productivity (Table 2.1).

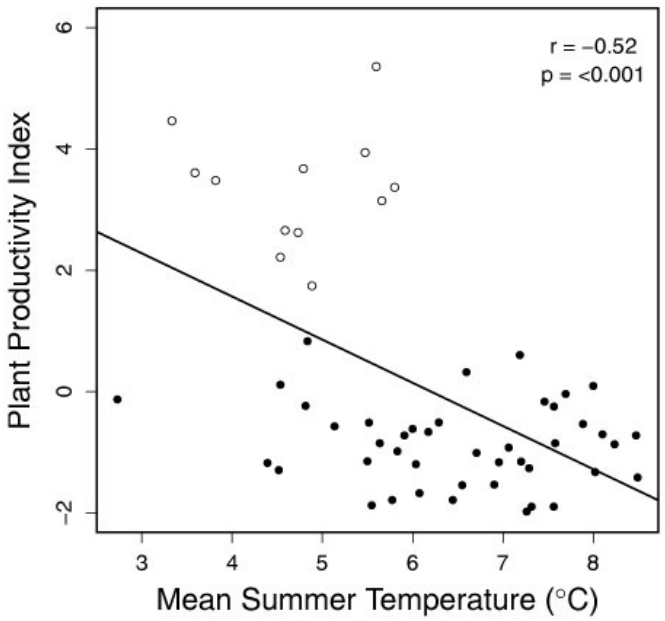

Figure 2.15: Bivariate relationship between plant productivity index and mean summer soil temperature. The solid line represents a linear model including all points in the figure (n = 55 plots). Tall shrubs are represented by open circles (n = 12 plots) with all other vegetation types represented by closed circles (n = 43 plots).

2.4 DISCUSSION

There were three important findings within the observed patterns found in this study. First, I did not find evidence for a direct correlation between soil temperature and total soil nitrogen. Second, I found that soil nitrogen was the most important determinant of plant productivity, followed by soil moisture, and that soil moisture was strongly correlated with both soil temperature and soil nitrogen. Third, the data indicated that tall shrub plots had higher productivity than the other vegetation types at the same level of environmental conditions and that tall shrub productivity was strongly linked to mean soil temperature. These results indicate that soil moisture likely plays an important role in moderating plant productivity and soil nitrogen, and that soil moisture is the probable link between soil temperature and soil nitrogen. These results also indicate that tall shrubs may have a competitive advantage over other vegetation types with increasing soil temperatures.

2.4.1 Environmental Relationships

The variation in total nitrogen was high in this study and cannot be attributed solely to differences between vegetation types. Frost boil habitats had significantly lower nitrogen levels than the other vegetation types and showed little variation while the other vegetation types did not differ. This can likely be attributed to the differences in the proportion of organic and mineral soil in the samples, as there was little to no organic layer present in frost boil habitats. The frost boil habitat plots had values between 611 and 3917 mg N kg^{-1}, which is lower than values describing mineral soils at in alpine heath tundra near Abisko, Sweden (2000 to 10000 mg N kg^{-1}; Sundqvist *et al.* 2011) but similar to those for mineral soil dominated sites in the Canadian High Arctic (991 and 3700 mg N kg^{-1}; Banerjee *et al.* 2011). The majority of the total

nitrogen values for the other vegetation types were around 10000 mg N kg^{-1}, which is similar to a dry heath in the southern arctic ecoregion of Canada (11100 mg N kg^{-1}; Chu and Grogan 2010) and an organic High Arctic site (10680 mg N kg^{-1}; Banerjee *et al.* 2011). The more extreme values are closer to those experienced in birch tundra (15800 and 17900 mg N kg^{-1}; Chu and Grogan 2010).

Soil temperatures have been found to be strongly linked with incoming solar radiation (Beltrami and Kellman 2003). However, this study found only a weak link between soil temperature and incoming solar radiation, estimated here as heat load. The amount of incoming solar radiation is dependent on the aspect; in the northern hemisphere south-facing slopes receive more direct incoming solar radiation than north-facing slopes due to the angle the sun is in relation to the earth (Allen et al. 2006). Examination of north- vs. south-facing slopes shows that higher soil temperatures were located on south-facing slopes, but there was much overlap between the temperatures. Soil temperature also could not be fully predicted by vegetation type which is consistent with soil temperature also being affected by factors such as vegetation cover, which alters incoming solar radiation (Zhang et al. 2001).

Previous experimental studies in the arctic have found increased nitrogen with increased soil temperatures (e.g., Hartley *et al.* 1999, Rustad *et al.* 2001, Aerts *et al.* 2006), but that was not the case in this study. There were no significant correlations between either mean soil temperature or soil temperature coefficient of variation and total soil nitrogen. Soil samples taken in 2010 from 20 of the study plots, analyzed for both total and inorganic (nitrate + ammonium) soil nitrogen, indicates that there was a significant positive correlation between total soil nitrogen and inorganic nitrogen (data not shown; $r = 0.84$, $p = <0.001$). Increases in

inorganic nitrogen were the most noticeable above total nitrogen values of 15000 mg N kg^{-1}. While inorganic nitrogen tends to increase with total nitrogen, there is much less inorganic nitrogen present in the soil than total nitrogen, and the relative proportion of inorganic nitrogen to total nitrogen is lower in arctic and alpine soils as compared to temperate soils (Callaghan *et al.* 2004). This may explain the lack of a significant relationship between soil temperature and total nitrogen. Studies that found a relationship between nitrogen and soil temperature evaluated inorganic nitrogen and net nitrogen mineralization rates (e.g., Binkley *et al.* 1994, Hartley *et al.* 1999, Weedon *et al.* 2012). Differences in inorganic nitrogen may be masked by the much larger total nitrogen values, particularly because at this site inorganic nitrogen values were relatively similar when total nitrogen values were below 15000 mg N kg^{-1}, which includes 52 of the 60 measured plots. Most plants have a preference for inorganic nitrogen, although some arctic species take up organic nitrogen (Schimel and Bennett 2004, Nasholm *et al.* 2009), so measurements of the total soil nitrogen pool may not be sufficiently sensitive to capture the true potential of inorganic nitrogen to limit plant productivity.

Soil moisture has been linked with different aspects of soil nitrogen in many studies. Microbial activity and biomass (Prado and Airoldi 1999, Illeris *et al.* 2003), decomposition (Robinson *et al.* 1995), inorganic nitrogen (Banerjee *et al.* 2011), net nitrogen mineralization (e.g., Binkley *et al.* 1994, Shaw and Harte 2001, Chu and Grogan 2010), and nitrification (Shaw and Harte 2001) have all been shown to increase with soil moisture. This study found a significant positive correlation between soil moisture and total nitrogen. High levels of soil moisture can inhibit soil processes, especially in cold temperatures (e.g., Nadelhoffer *et al.* 1992, Prado and Airoldi 1999). However, there is no indication in this data that high soil

moisture is limiting these processes. Generally soil moisture is lower on higher elevation and steeper slopes than lower elevations or shallower slopes (e.g., Western *et al.* 1999, Janowicz *et al.* 2004, Penna *et al.* 2009), and the alpine regions of the Wolf Creek basin experience a reduction of soil moisture through the summer months (Janowicz et al. 2004). The correlation between soil moisture and total soil nitrogen could indicate that increased soil nitrogen was due to a reduction in nitrogen cycling rates, and thus more nitrogen was present in the soil due to less plant nitrogen uptake. However, the significant positive correlation between soil moisture and plant productivity leads me to believe this was not the case, as I would expect productivity to be reduced if available soil nitrogen was reduced. The presence of a relationship between soil moisture and nitrogen, but not between soil temperature and nitrogen, might indicate that at this site soil moisture is more important for microbial activity and nitrogen turnover than soil temperature is. While soil moisture was strongly correlated to total nitrogen, the strength of the relationship between total nitrogen and total carbon, a proxy for organic content, indicates that increases in total nitrogen at this site are more likely due to higher organic content in the soil. As discussed above, a different measurement of nitrogen, such as inorganic nitrogen or nitrogen cycling rates, would provide stronger evidence of the importance of soil moisture for microbial activity and nitrogen turnover.

This study found significant relationships between soil moisture and the soil temperature measurements, which could be the result of both direct and indirect interactions between these environmental variables. Soil moisture can directly affect soil temperatures through evaporative cooling (Zhang *et al.* 2001), but it can also affect soil temperature indirectly. Increased soil moisture has been associated with increased vegetative cover (Walker *et al.*

1993), and taller vegetation tends to trap snow (Pomeroy *et al.* 2006). Thus, snow cover had similar associations with soil temperature as soil moisture, but the relationships were stronger between snow cover and soil temperature. This study found significant correlations between the presence of taller vegetation with increased soil moisture (data not shown; $r = 0.47$, $p = <0.001$) and increased snow depth with taller vegetation (data not shown; $r = 0.41$, $p = 0.010$) when late-lying snow bed plots were excluded from the analyses. During the summer the vegetation shades the soil and reduces convective heat transfer (Blok *et al.* 2010) while during the winter the snow also serves as an insulating layer (Wundram *et al.* 2010). Thus, soil moisture likely plays a role in decreasing the temperature range of the soil through evaporative cooling in the summer and the insulating effects of vegetation trapping snow during the winter. The increase in winter soil temperatures would also raise the mean soil temperature, due to the summer cooling effect of soil moisture being smaller than the insulating effect of snow during the winter (Zhang *et al.* 2001). Other studies found sites with high soil moisture in the summer and thicker snow during the winter tended to have smaller temperature variation than other sites (Wundram *et al.* 2010). While both the coefficient of variation of soil temperature and mean soil temperature were significantly correlated with soil moisture, the strength of the correlation was much stronger between soil moisture and the soil temperature coefficient of variation.

Considering that soil moisture and snow depth both had similar relationships with soil temperature, it is surprising that they did not have a significant correlation with each other. Snow cover provides moisture during thaw events, and increased snow cover with later melt dates increase the time of soil saturation (Buckeridge and Grogan 2010). The amount of water

infiltration into the soil due to snow melt is affected by frozen soils. Factors such as soil texture and water saturation during freezing affects the capacity of soils to absorb and store melt water (Gray et al. 2001). Additionally, soils often undergo cycles of freezing and thawing during the snowmelt period (Brooks et al. 1998), which will also affect water infiltration. However, the soil samples taken in this study, 30 June and 17 July, were probably collected late enough in the season that the soil moisture content was more a function of slope position, local topography, and recent precipitation than snow. Similarly there was no relationship between soil nitrogen and snow cover. Nitrogen can be deposited from the snowpack, but the majority of nitrogen released during snow melt is from lysing microbes due to freeze-thaw cycles under the snow (Buckeridge and Grogan 2010). These nutrients may be quickly assimilated by both plants and microbes, and thus not be detectable later in the season.

2.4.2 Plant Productivity Relationships

Plant productivity was significantly related to all environmental variables except snow cover. Plant productivity showed the strongest correlations with total nitrogen with all vegetation types included and when tall shrubs were excluded from the analyses. As discussed above, total nitrogen is positively correlated with inorganic nitrogen, and thus plots with higher total nitrogen would likely also have higher plant available nitrogen. Nitrogen is the most limiting nutrient in arctic and alpine environments (e.g., Shaver and Chapin 1980, Nadelhoffer et al. 1992, Atkin 1996), and so increased productivity with increased nitrogen is to be expected. However, the amount of nitrogen in the plots can also be affected by the vegetation present. The increase in total nitrogen could be a result of increased quantity and quality of litter inputs. The rate of decomposition can also change with the composition of the vegetation

where more productive plots contain greater abundances of species whose tissues have faster decomposition rates, such as graminoids and deciduous shrubs (Robinson 2002). This may be the case in this study, since there were significant correlations between productivity and graminoid and deciduous shrub abundance (data not shown; $r = 0.60$, $p = <0.001$ and $r = 0.91$, $p = <0.001$, respectively). These strong correlations could also be due to tall shrub habitats being much more productive and having more deciduous shrubs and graminoids than other vegetation types.

Soil moisture had the second strongest relationship with plant productivity, followed by soil temperature. This is different from previous findings that soil temperature was more important than soil moisture in determining vascular plant biomass in both wet and dry arctic tundra (Bardgett et al. 2007). This is likely due to differences in the limiting factors at my study site. The findings of this study are consistent with other research that found soil nitrogen to be the most limiting factor for plant growth (e.g., Shaver and Chapin 1980, Nadelhoffer et al. 1992, Atkin 1996). This study cannot determine if the hierarchy of limiting factors is the same as the order of the relationships found here, soil nitrogen followed by soil moisture and then soil temperature. Soil moisture was also strongly correlated with soil nitrogen, which is consistent with the importance of moisture levels for decomposition and nitrogen turnover (Nadelhoffer *et al.* 1992). These relationships indicate that the indirect effects of climate change on soil nitrogen and early summer soil moisture might be more important for changes in plant productivity at this site than simply warmer temperatures alone.

There was no significant correlation between plant productivity and snow depth. This was initially surprising considering the number of studies that have found a positive relationship

between snow cover and vegetation cover (e.g., Pomeroy *et al.* 1999, Sturm *et al.* 2001, Pomeroy *et al.* 2006). Although non-significant, the direction of the correlation between plant productivity and snow depth would have been negative without the tall shrubs included in the analysis. This might be because without the tall shrubs, which collect snow, the late-lying snow beds experience the deepest snow. These plots tend to take the longest for snowmelt, and thus have a much shorter growing season and less opportunity to increase their productivity. There was a significant correlation between snow depth and canopy height (data not shown, $r = 0.41$, $p = 0.010$) and between productivity and snow depth (data not shown, $r = 0.34$, $p = 0.035$) when late-lying snow bed plots were removed from the analyses.

Tall shrubs consistently sorted out separately from the other vegetation types with regards to plant productivity. Tall shrubs experienced higher productivity at similar levels of all environmental factors as compared to the other vegetation types. This pattern was consistent with the initial examination of vegetation types, where tall shrub plots generally had values that fell in the middle of the measured environmental variables, but had noticeably higher productivity than the other vegetation types. Removal of tall shrub plots from the analyses strengthened all the correlations of abiotic factors with plant productivity, except soil temperature coefficient of variation which became non-significant. The negative correlation between soil temperature coefficient of variation and plant productivity only when tall shrubs were included in the analysis was probably due to the greater moderating effect of tall shrubs on soil temperatures in both the summer and winter, where tall shrubs shade the soil in the summer, and retain insulating snow in the winter. This moderating effect of shading can also be seen in the negative correlation between mean summer soil temperature and plant

productivity, with all vegetation types included in the analysis. Mean summer soil temperature showed the opposite relationship with productivity as compared to mean annual soil temperature, which is consistent with the positive relationship of summer soil temperature with soil temperature coefficient of variation (data not shown, $r = 0.76$, $p = <0.001$). As discussed above, the tall shrub plots experienced generally lower summer soil temperatures, as well as lower coefficients of variation, as compared to other vegetation types due to summer shading of the soil. The negative correlations between soil temperature coefficient of variation and plant productivity, although significant only with all vegetation types included, indicates that productivity was higher in plots that experienced less extreme temperature fluctuations throughout the year. Thus, plots that had very high mean summer soil temperatures tend to also have high soil temperature coefficients of variation, and lower productivity.

Tall shrubs have been found to alter their environment (Myers-Smith *et al.* 2011), which may explain the consistent difference between the productivity of tall shrubs and the rest of the vegetation types. As discussed above, tall shrubs alter soil temperatures through summer shading (Blok *et al.* 2010) and trapping snow in the winter (Pomeroy *et al.* 2006). Trapped snow increases the spring nutrient pulse (Buckeridge and Grogan 2010) and summer moisture (Sturm *et al.* 2001). These changes to temperature, nutrient inputs, and soil moisture can increase microbial activity in both winter and summer, increasing available nitrogen levels (Binkley *et al.* 1994, Buckeridge and Grogan 2008). As well this trapped snow protects vegetation against winter wind and frost damage (Sturm *et al.* 2001). Tall shrub litter is also of higher quality than surrounding low shrub tundra, which increases decomposition (Buckeridge *et al.* 2010). The

different productivity levels within tall shrub habitats could be a result of a favorable interaction of various factors in a modified environment.

The only significant correlation of tall shrub habitat productivity was with mean soil temperature, which could indicate that tall shrubs are limited by soil temperature at the Wolf Creek study site. The relationship between mean soil temperature and tall shrub productivity was due to strong correlations with both spring and fall mean soil temperatures (data not shown, $r = 0.69$, $p = 0.014$ and $r = 0.69$, $p = 0.013$, respectively), but not summer or winter temperatures. The strong correlation of tall shrub productivity with mean soil temperature is different from the other vegetation types, which were more related to soil nitrogen and soil moisture. The difference in productivity between tall shrubs and other vegetation types is possibly due to the modified environment experienced by tall shrubs. I expected tall shrubs to show significantly different values of the abiotic factors measured as compared to the other vegetation types if environmental modification was occurring. However, these modifications are likely to be more subtle than could be detected with this study. In particular, the measurements of soil nitrogen and moisture in this study could be unable to detect subtle differences between plots, as discussed above.

The higher productivity of tall shrubs at the same environmental variable levels as other vegetation, and the significant correlation between tall shrub productivity and mean soil temperature indicates the possibility that with warming temperatures tall shrub habitats have the ability to expand into areas now occupied by other tundra vegetation, and outcompete the vegetation currently present. Their higher productivity is likely due to their ability to alter their own environment, which could result in a positive feedback loop of a more suitable

environment for shrubs, reinforcing shrub growth and expansion (Sturm *et al.* 2005, Myers-Smith *et al.* 2011). Retrospective studies assessing vegetation change over the last approximately 50 years found many cases of increased shrub growth across the circumpolar arctic and in alpine environments (e.g., Tape *et al.* 2006, Hallinger *et al.* 2010, Myers-Smith *et al.* 2011). The expansion of shrubs has been linked to climate change through experimental climate change studies that found shrub growth is highly responsive to, and is increasing in abundance with, alterations to the environment similar to those that are expected with climate change. Experimental climate change studies have often found that deciduous shrubs were the most responsive to long-term warming and fertilization (e.g., Shaver *et al.* 2001, Dormann and Woodin 2002, Walker *et al.* 2006). The highly responsive nature of tall shrubs to climate change scenarios found in other studies, as well as the different relationships between tall shrub productivity and abiotic factors as compared to the other vegetation types in this study, may indicate that tall shrubs could have a long-term advantage over other vegetation types at this study site with increasing temperatures.

2.4.3 Conclusion

The observed patterns (Fig 2.16b) between environmental variables and plant productivity differed slightly from those I hypothesized (Fig 2.16a). Not all hypothesized relationships were observed at this site, but the directions of the observed correlations were accurately predicted. I found that the environmental factor most strongly correlated with plant productivity, of all vegetation types and with tall shrub habitats excluded, was soil nitrogen, which is consistent with previous studies that found nitrogen to be the most limiting factor at arctic and alpine tundra sites (e.g., Shaver and Chapin 1980, Nadelhoffer *et al.* 1992, Atkin 1996). This finding

also supports the theory that indirect effects of climate change on nutrient availability will show the greatest effect on plant productivity (e.g., Chapin 1983, Chapin *et al.* 1995, Brooker and van der Wal 2003). However, changes in nitrogen are often viewed as an indirect effect of changing temperatures (e.g., Chapin 1983, Chapin *et al.* 1995, Brooker and van der Wal 2003). In this study I found a strong correlation between total soil nitrogen and soil moisture, but none between nitrogen and soil temperature. Soil moisture was also significantly correlated with plant productivity and soil temperature.

Tall shrub habitats were different than all other vegetation types with regards to plant productivity. I found that tall shrubs had higher productivity than other vegetation types at similar levels of environmental variables, and that tall shrub habitat productivity was strongly related to mean soil temperature, but no other environmental variables. This higher productivity might explain why tall shrubs have been found to be expanding across arctic and alpine tundra with increasing temperatures (e.g., Tape *et al.* 2006, Hallinger *et al.* 2010, Myers-Smith *et al.* 2011). Their ability to alter their own environment reinforces tall shrub growth, and their high productivity could allow them to persist over other vegetation.

While causality cannot be inferred from the correlations discovered in this study, they can be used to generate hypotheses about controls on plant productivity. These results indicated that while soil nitrogen had the strongest relationship with productivity of most vegetation types, spring and fall mean soil temperatures were strongly correlated with tall shrub productivity. Early summer soil moisture might also be important for plant productivity, both directly and through its relationship with soil nitrogen. Thus vegetation responses to climate change at this site could differ depending on which environmental factor experiences the

greatest changes. Increases in soil temperature could result in increased tall shrub growth and expansion, while increases in summer soil moisture would more likely result in increased growth of the other vegetation types.

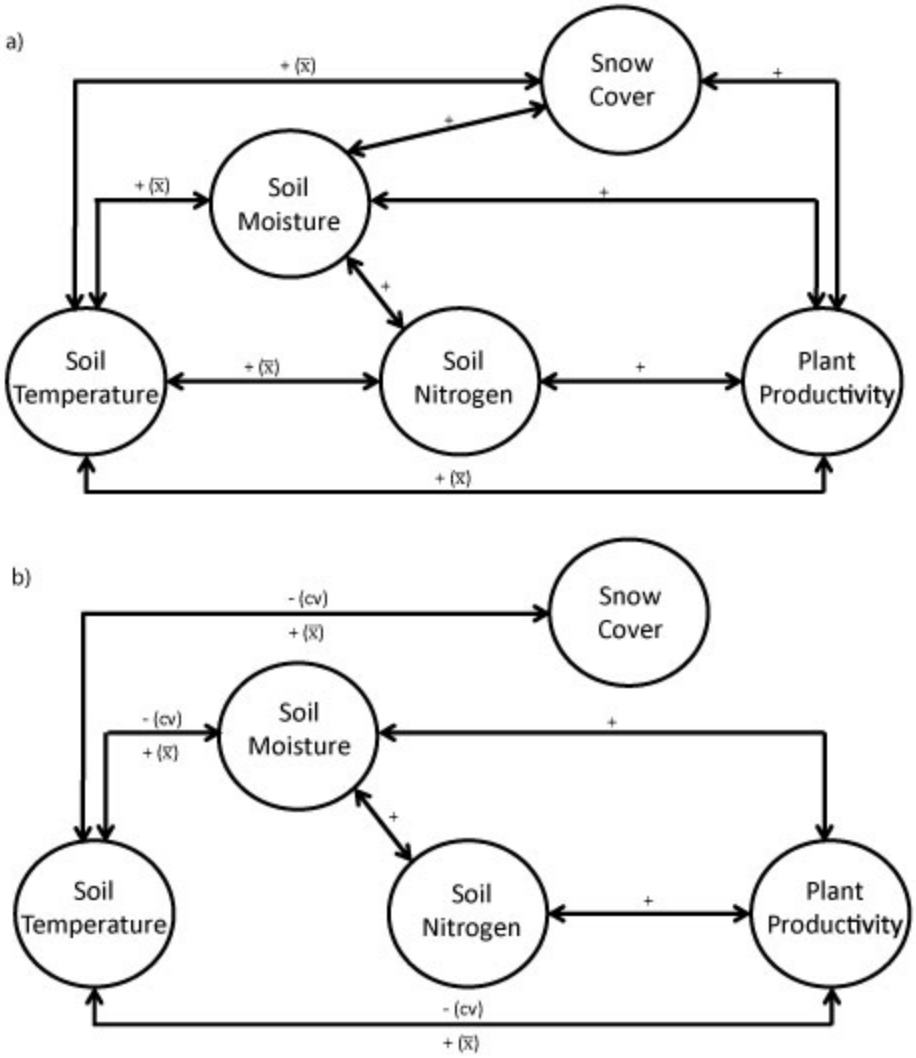

Figure 2.16: Conceptual diagram showing (a) hypothesized and (b) observed correlations between environmental variables and plant productivity along a natural vegetation gradient. The positive and negative symbols represent the direction of the correlations, indicating positive or negative correlations between two variables, respectively. Double headed arrows represent the possibility of bi-directional relationships. The abbreviation $\bar{x}$ stands for mean soil temperature and cv stands for the coefficient of variation of soil temperature.

3.0 INITIAL EFFECTS OF EXPERIMENTAL SOIL WARMING AND FERTILIZATION ON PLANT PRODUCTIVITY

3.1 INTRODUCTION

Arctic and alpine environments are experiencing accelerated climate change as compared to the rest of the world, with projected increases of 2.5°C in the next 50 years (ACIA 2005, Solomon et al. 2007). This has made the Arctic into a study area of increased importance with regards to climate change. Plants in cool northern environments are sensitive to the effects of increased temperatures (Aerts *et al.* 2006), and changes to plant community composition are expected as a result (Epstein *et al.* 2000, ACIA 2005). However, changes in the productivity of current plant species are expected to occur prior to shifts in community composition.

Recent studies have indicated that soil temperature may play a more important role than air temperature in regulating changes in plant productivity (e.g., Brooker and van der Wal 2003, van Wijk *et al.* 2003, Natali *et al.* 2012). It has also been suggested that these changes in plant productivity are tied to the indirect effects of temperature on nutrient availability, not simply warmer temperatures alone (e.g., Chapin 1983, Chapin *et al.* 1995, Brooker and van der Wal 2003). Previous research at Wolf Creek found that 10 years of temperature manipulation using open topped chambers produced few significant effects on plant productivity, and that natural annual temperature variations also showed little consistent effects on plant productivity (Pieper *et al.* 2011). These authors concluded that plant growth was more likely to be limited by soil factors than temperature. This study, located in close proximity to the Pieper *et al.* (2011) study, focuses on the initial responses of experimental soil warming and fertilization on plant productivity in low shrub alpine tundra.

While increasing air temperatures have been the focus of much climate change research, soil temperature will also be affected by climate change since increases in air temperature can

be transferred to the soil due to conductive heat transfer (Beltrami and Kellman 2003). Despite this link to air temperatures, soil temperature is also affected by incident solar radiation, vegetative cover, snow cover, and soil moisture (Zhang *et al.* 2001). Plant productivity can increase with increased soil temperature through an increase in photosynthetic ability, growth rate, or nutrient uptake (e.g., Chapin 1983, Bassirirad 2000, Rustad *et al.* 2001). Increased soil temperature also indirectly affects plant productivity through increased nutrient availability (Rustad *et al.* 2001). The rate of nutrient input is low in arctic environments, with inputs coming from precipitation, atmospheric deposition, and nitrogen fixation (Chapin 1983). Nutrient cycling in arctic and alpine tundra is slow and constrained by low soil temperature and moisture (e.g., Jonasson *et al.* 1999a, Wu *et al.* 2006, Currie *et al.* 2010), with nitrogen often the most limiting nutrient for plant growth (e.g., Shaver and Chapin 1980, Nadelhoffer *et al.* 1992, Atkin 1996). Thus, increases in plant available nitrogen will occur primarily through an increase in nitrogen cycling rates, with decomposition and net mineralization increasing with increased soil temperature (Robinson 2002).

Many studies on climate change focus on manipulating temperature; however, few studies have specifically assessed the effects of manipulating soil temperature on plant productivity in arctic or alpine tundra (but see Hartley *et al.* 1999, Brooker and van der Wal 2003, Natali *et al.* 2012). This is despite the fact that many studies found that as they manipulate air temperature, soil temperature also changes (e.g., Chapin *et al.* 1995, Jonasson *et al.* 1999b, Klanderud 2008). Increases in vegetative growth have been associated with an initial response to air warming experiments (Arft *et al.* 1999). Warming studies, of both air and soil, have indicated that an increase in vascular plant aboveground biomass can be expected with increased temperatures

in arctic environments (e.g., Rustad *et al.* 2001, Walker *et al.* 2006, Elmendorf *et al.* 2012b), particularly graminoids and deciduous shrubs (e.g., Chapin *et al.* 1995, Dormann and Woodin 2002, Walker *et al.* 2006). Increases in plant biomass are also associated with increased nutrients, where fertilization studies indicate that plants respond most strongly to nitrogen additions than to other nutrients (e.g., Shaver and Chapin 1980, Chapin *et al.* 1995, Jonasson *et al.* 1999b). Similar changes in plant communities are being observed outside of experimental manipulations, with increasing abundance of graminoids in northern Quebec (McManus *et al.* 2012) and shrubs in Alaskan, Canadian, and Russian Arctic tundra (Myers-Smith *et al.* 2011). Numerous studies have stressed the importance of indirect effects of climate change via changes in soil processes, but there are still gaps in our understanding of such effects, particularly in separating out soil temperature from air temperature effects.

The objectives of this study were to determine the initial effects of manipulating soil temperature and nitrogen pools on plant productivity, as well as to see if increasing soil temperature affects nitrogen levels. If nitrogen availability was the primary factor limiting plant growth in this environment, then plant productivity should increase with fertilization. Alternatively, slow plant growth might constrain plant responses so that only those species with the greatest plasticity would show a response following a single season of fertilization. I also hypothesized that if soil warming increased net nitrogen mineralization, then inorganic nitrogen should show an increase in warmed plots, if not the increase in inorganic nitrogen could be masked by a concurrent increase in plant or microbial nitrogen uptake. Much of the previous research on climate effects on vegetation have focused on changes in air temperatures; this study will provide a new contribution by using a unique solar powered soil warming system that

is useful for remote locations to specifically assess how changes in the soil environment affect plant dynamics.

3.2 METHODS

3.2.1 Study Area

The study area (N 60°33'45.0", W 135°07'57.3", 1551 m asl) is located within the Wolf Creek drainage basin approximately 19 km from the city of Whitehorse, Yukon. The experimental study site is a 50 x 50 m area of gently sloping (approximately 3°) high latitude alpine tundra with a southern aspect, just below an alpine ridge. The study area falls within the discontinuous/sporadic permafrost zone (Brown *et al.* 2001). The soil is classified as Orthic Eutric Brunisols; the underlying geography of the area is mainly sedimentary in nature and is overlain by gravelly till with depths ranging up to 2 m, while the surface topography consists of shallow hummock-hollows (Janowicz 1999). This area experiences a sub-arctic climate, which includes low relative humidity, low precipitation (300-400 mm annually with approximately 50% falling as rain), and large annual temperature variations with cool summers (mean monthly temperatures 5°C to 15°C) and cold winters (mean monthly temperatures -10°C to -20°C; Wahl *et al.* 1987, Janowicz 1999).

The site is located within the Boreal cordillera ecozone in the Yukon southern lakes ecoregion (Smith *et al.* 2004). Vegetation in the experimental site is composed of a low-shrub tundra community that is floristically similar to arctic tundra. Dominant plant species include *Dryas octopetala* L. (eightpetal mountain avens), *Salix arctica* Pall. (arctic willow), *Salix reticulata* L. (netleaf willow), *Polygonum viviparum* L. (syn. *Bistorta vivipara* (L.) Delarbre) (alpine bistort), *Lupinus arcticus* S. Watson (arctic lupine), herbs and graminoids such as

Pedicularis lanata Cham. & Schltdl. (woolly lousewort) and *Carex microchaeta* T. Holm (smallawned sedge), as well as lichens such as *Cetraria* species, and mosses such as *Polytrichum* species. Taxonomic nomenclature follows the Integrated Taxonomic Information System online database (ITIS 2012).

3.2.2 Study Design

Soil warming and nitrogen fertilization treatments were applied in a randomized block factorial design to 24 plots with six replicates of each treatment (warming, fertilization, warming + fertilization, and control; Fig 3.1). Each plot was 1 m^2, with a minimum distance between plots of 2 m, to reduce the likelihood of treatment effects reaching a neighbouring plot (Bret-Harte *et al.* 2001). The study was blocked along the dominant spatial axis rather than along the slope, because previous studies at this site have shown no evidence of gradients in plant growth along the slope (Pieper 2010). Boardwalks were constructed in high traffic areas along the plots to reduce surface disturbance from sampling activities.

The aim of the warming treatment was to increase soil temperatures by 2°C above ambient temperatures during the growing season (early-June to late-August). A 2°C increase was chosen as an appropriate increase in soil temperature that might result from the predicted increase in air temperature of 3.7°C for the Arctic during the next century (Chapin *et al.* 1995, ACIA 2005). The heating occurred by using solar powered heating probes inserted vertically into the ground to approximately 15 cm depth to capture the depth of the rooting zone. The use of vertical heating probes instead of horizontal probes decreases soil, microbial, and root disturbance caused by inserting the probes (Aronson and McNulty 2009). Each plot undergoing the warming treatment had 100 heating probes inserted in a 10 cm x 10 cm grid. Three CR1000 dataloggers

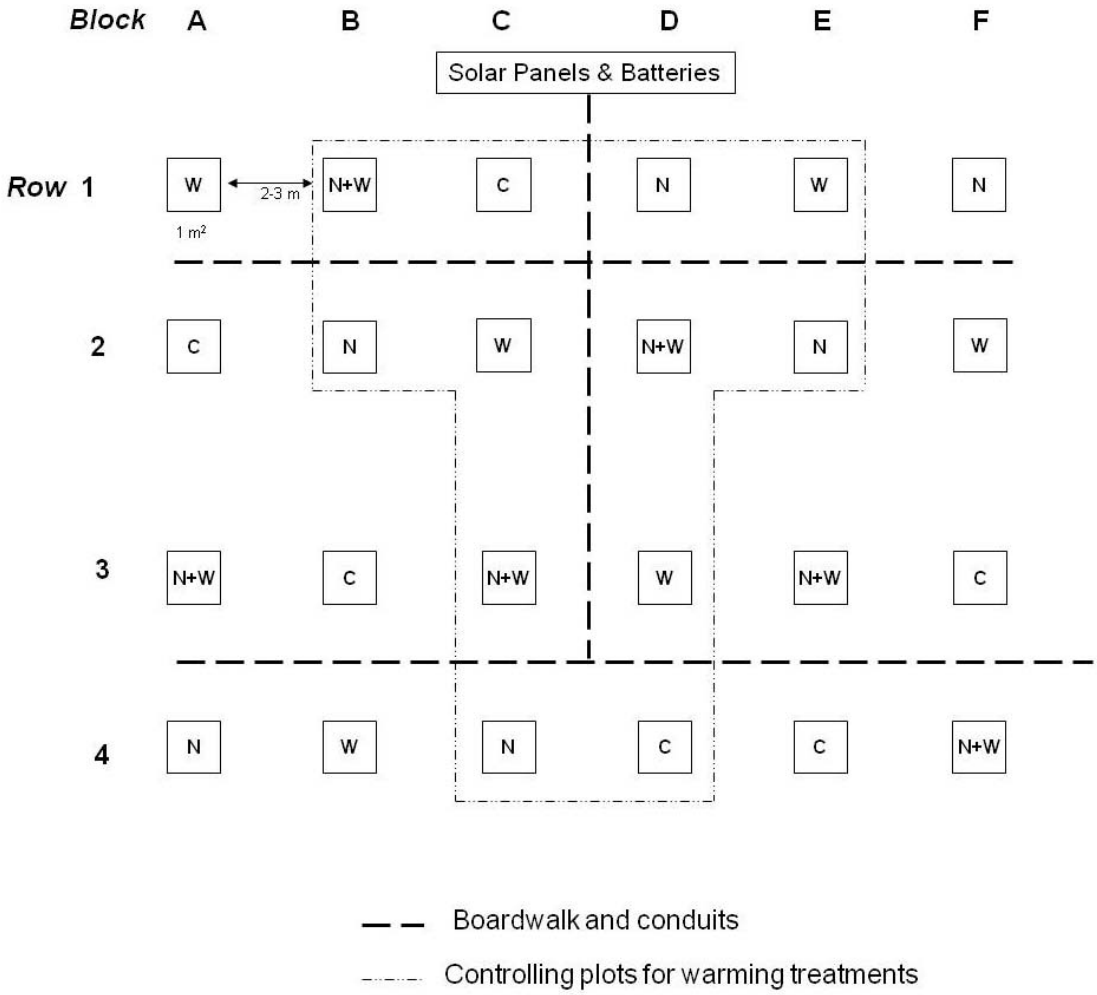

Figure 3.1: Schematic diagram of the site layout at the Wolf Creek study site, showing the arrangement of plots (squares) within experimental blocks. Letters within each square indicate the treatment to be applied (W = warming, N = fertilization, N+W = warming + fertilization, C = control). The controlling plots were connected to the monitoring and control datalogger; soil temperatures were recorded in these plots and used to control the heating system.

(Campbell Scientific, Edmonton, AB) monitored the temperatures of the plots and controlled power to the probes as necessary to maintain the target temperature during the snow free season. This method allowed for active control of the level of soil heating, while still being feasible in remote locations since it did not require a power grid connection. A trial warming period in 2010, from 8 July to 8 August, was used to debug the system and ensure the warming treatment was working, and the 2011 warming treatment was applied from 24 May to 1 September 2011.

With the fertilization treatment, the aim was to double the inorganic nitrogen pools in the near surface soil. This is a more environmentally appropriate rate of fertilization than applying a specific amount with no regard to the current levels of nitrogen. During the preliminary field season trials were run that tested three types of fertilizer application, wet application of ammonium-nitrate (NH_4NO_3), dry application of NH_4NO_3, and slow release urea pellets in 0.25 m^2 plots against control plots. The application rate for all fertilizer types was 1 g N m^{-2}. The wet application of NH_4NO_3 was dissolved in 25 ml water. The fertilizer trial showed a trend of increased nitrate-nitrogen levels between the control plots and the dry application of NH_4NO_3. The dry application also had significantly higher nitrate-nitrogen as compared to all other application types. There was no significant difference between ammonium levels for the controls or any of the fertilizer treatments, however the dry application did show the highest levels of ammonium. Following these trials dry NH_4NO_3 at a rate of 2 g N m^{-2} was chosen as the fertilizer to ensure a stronger fertilizer response than what we achieved in the trials with 1 g N m^{-2}. The fertilization treatment was applied to the experimental plots on 15 June 2011, with the NH_4NO_3 crystals spread evenly over the plots.

3.2.3 Field Measurements

Soil temperature and nitrogen pool sizes were monitored in the experimental site to ensure that the warming and fertilization treatments caused a change in the variables of interest, temperature and soil nitrogen respectively. Soil temperature was monitored in six control and six warming plots, which were used for control of the solar powered warming system (Fig 3.1). Temperature was monitored using an average temperature from three type "T" thermocouples (copper-constantan, Omega Engineering Inc, Stamford, CT) per plot, each at 10 cm depth. Temperature data were sampled every minute and an average over 15 minutes was recorded. Temperature data were recorded for a trial warming period in 2010, from 8 July to 9 August 2010, and for the entire period of warming in 2011, 24 May to 1 September 2011.

Nitrogen pool sizes prior to the start of the experiment were determined from bulk soil samples collected on 15 and 16 July in the 2010 field season. These were collected from just outside the edges of the plots to avoid disturbing the vegetation. The samples were collected from multiple vegetation types that were present within each plot from the organic and mineral horizons. Ion exchange resins (Mixed Bed Exchange Resin, IONAC® NM-60 H/OH± Form, Type I, Beads; Qian and Schoenau 2002) were used to assess inorganic nitrogen availability, ammonium (NH_4^+) and nitrate (NO_3^-), following the initial fertilization treatment in 2011. Resin bags, nylon bags containing 10 g dry weight ion exchange resin, were buried in the upper 5 cm of mineral soil 15 June 2011, immediately prior to fertilization. This was to ensure that any nitrogen adsorbed to the resins were the result of nitrogen moving through the soil, not from direct contact with NH_4NO_3 crystals. The bags were removed 13 August 2011 and stored in

refrigerated conditions until analysis. Due to issues with the shipping and supply of ion exchange resins, only one resin bag was placed in each plot.

I measured short term plant productivity responses of individual species. I selected six species that were abundant at the site, 3 prostrate shrubs: *Dryas octopetala* (mountain aven, semi-evergreen), *Salix arctica* (arctic willow, deciduous), and *Salix reticulata* (net-leaved willow, deciduous); two forbs: *Polygonum viviparum* (alpine bistort), and *Lupinus arcticus* (arctic lupine); and one graminoid: *Carex michrochaeta* (small-awned sedge). Productivity was measured using the dimensions of individual leaves, including leaf width, leaf length, petiole length, and number of leaves depending on the species (Table 3.1). Specific leaf area (SLA), the one-sided area of a fresh leaf divided by its dry mass (Cornelissen *et al.* 2003), was also calculated for the leaves on which plant productivity measurements were taken. Leaves were randomly selected throughout the entire plot with a minimum distance of 10 cm between samples. Some species occurred in clumps or were rare, not allowing for 10 cm spacing, so leaves were selected at the maximum distance possible to try to get samples from different individuals/ramets. Due to the long-term nature of the experimental plots, large quantities of leaves could not be taken from the plots without damaging the productivity of the plants for future years. Thus SLA for most species had to be based upon a smaller sample of leaves than is suggested (n = 10; Cornelissen *et al.* 2003). There were missing data for both the leaf measurements and SLA (Table 3.2) due to a species being missing or rare in a plot. *P. viviparum* was not sampled for SLA in any plots due to its low abundance.

Table 3.1: Leaf measurements of the study species used to assess plant productivity responses to experimental treatments.

	Leaf Length	Leaf Width	Petiole Length	Number of Leaves
P. viviparum	X	X		X
L. arcticus	X	X	X	
S. arctica	X	X		
S. reticulata	X	X		
D. octopetala	X	X		
C. microchaeta	X			

Table 3.2: Summary of missing samples for leaf measurements (LM) and specific leaf area (SLA) for each treatment combination (baseline n = 6 per treatment).

		Control	Fertilized	Warmed	Fertilized + Warmed
P. viviparum	LM	0	1	0	0
L. arcticus	LM	0	0	1	1
	SLA	1	0	2	1
S. arctica	LM	0	0	0	2
	SLA	1	3	0	3
S. reticulata	LM	1	1	0	0
	SLA	2	1	0	1
D. octopetala	LM	0	0	0	0
	SLA	0	0	0	0
C. microchaeta	LM	1	2	1	0
	SLA	2	3	1	0

3.2.4 Laboratory Methods

All soil samples were oven dried at 105 °C for 48 hrs to determine gravimetric soil moisture. The samples were then passed through a 2 mm sieve to remove rocks and homogenize the sample. A 2 to 6 g sub-sample of soil was taken from 2010 nitrogen pool samples to be further homogenized and reduced to a fine powder using a ball mill for 24 hrs and then processed for total nitrogen. These sub-samples were analyzed concurrently for total carbon and total nitrogen using a TruMac CN (LECO, St. Joseph, MI) giving total nitrogen as a percent of sample dry weight. Total nitrogen values were converted into milligrams nitrogen per kilogram of dry soil (mg N kg^{-1}) before further analysis.

Inorganic nitrogen was assessed from both the 2010 nitrogen pool samples and the 2011 ion exchange resins using a 2M KCl extraction procedure (Maynard *et al.* 2008). A portion of the sieved soil samples were placed in 250 mL extraction bottles to maintain a 1:10 ratio of sample to elutant (e.g., 5 g : 50 mL). Each resin bag was gently washed to remove debris, and the contents of the each bag were placed in 50 mL of elutant. The soil samples and ion exchange resins were agitated for 30 min and 1 hr, respectively. The fluid extract was filtered using Whatman filter paper pre-leached with 2M KCl solution and then analyzed using a Discrete Chemistry Analyzer (Smartchem 200, Westco Scientific Instruments, Brookfield, CT) giving ammonium and nitrate in parts per million (ppm). Inorganic nitrogen values from the 2011 ion exchange resins were converted into microgram nitrogen per gram dry weight of resin (μg N g^{-1} dry weight resin) while those from the 2010 soil samples were converted into milligrams nitrogen per kilogram of dry soil (mg N kg^{-1}) before further analysis. Prior to nitrogen

conversions, the data were compared to the detection limits of the machines they were analyzed on, and all values lower than the detection limits were set to zero.

Leaves collected for SLA were photocopied shortly after collection to capture fresh leaf area. Different parts of the leaf were included for each species depending upon the collection procedure: *L. arcticus* included the leaflets but not the petiole; *S. arctica* and *S. reticulata* included both the leaf and the petiole; *D. octopetala* included the leaf, petiole and leaf sheath; *C. microchaeta* included the leaf blade and leaf sheath. The photocopies were used to determine leaf area using WinFolia (Reagent Instruments Inc., Ste-Foy, Quebec, Canada). Photocopies of shapes of known areas were used to determine the error associated with analyzing photocopies instead of fresh samples. No error due to photocopying was detected, and pixel differentiation was checked with each photocopy to control for darker or lighter photocopies affecting leaf area. The leaves were then dried at 60°C for 48 hrs and weighed at room temperature. The area of each leaf was then divided by the dry weight to get SLA (mm^2 mg^{-1}).

3.2.5 Statistical Analyses

All statistical analyses were performed in R (R Development Core Team 2011) and an α-level of 0.05 was used to assess statistical significance. Prior to analyses, data checking and unit conversions were performed. Plot level daily mean, minimum, and maximum temperatures were calculated over a 24 hour period, from 0:00 to 24:00 hours. All 2010 nitrogen values, total nitrogen, ammonium, and nitrate, were analyzed using plot level averages. Leaf measurements were also analyzed using plot level averages, while SLA was calculated for each species at the plot level.

To assess the effectiveness of the warming treatment to increase temperature by 2°C in warmed plots, temperature data were selected for analysis from the 12 plots used to control the warming treatment (Fig 3.1). The data analyzed spanned the 30 July to 5 August 2010 trial warming period as well as the same time period during 2011. This week was selected due to the fact that continuous warming occurred throughout this time, and it also contained both the warmest and coldest days during the 2010 trial warming. A mixed-effects model with temporal pseudoreplication (Crawley 2007) using the package 'nlme' (Pinheiro *et al.* 2012), was used to examine if soil temperature changed significantly with the warming treatment. The models were tested for autocorrelation structures in the data to account for the interdependence within the time series (Crawley 2007). All temperatures, except 2011 mean and minimum temperatures, fit a first-order autoregressive autocorrelation structure, corAR1. The 2011 mean and minimum temperature data fit an autoregressive moving average autocorrelation with a lag of 2, corARMA(q=2). There was no difference in the results of the mean or minimum temperature mixed effects models with either autocorrelation structure, so the data presented are the results from using corAR1 as the autocorrelation structure for all models. The 2011 minimum temperature model did not produce p-values, so an approximate p-value was calculated using the models test statistic and degrees of freedom.

An effect of blocking was tested for on the 2010 nitrogen data using an analysis of variance (ANOVA). The nitrate data was significantly different in two of the blocks ($F = 3.60$, $p = 0.004$), so blocking was included in all subsequent analyses. Treatment effects on inorganic nitrogen values collected from the post-treatment 2011 ion exchange resins were analyzed using ANOVAs (Crawley 2007). The ANOVAs were run using the *lme* function in the 'nlme' package

(Pinheiro *et al.* 2012) with Block fitted as a random factor, due to non-normal errors in the models fit with the ANOVA specific *aov* function. The *lme* function allows for correlated and unequal variances in the within-group errors (Pinheiro *et al.* 2012). The pre-treatment 2010 soil nitrogen samples were also assessed for differences using *lme* ANOVAs, to ensure that any differences found in the post-treatment 2011 soil nitrogen samples were a result of the treatments applied and not a pre-existing difference in nitrogen. The pre-treatment 2010 soil nitrogen samples were grouped by the treatments applied in 2011 to test for pre-existing differences. The organic and mineral horizons were analyzed separately. Variation in mineral soil horizon soil nitrogen between vegetation covers was visualized by plotting the raw data.

Plant productivity was assessed for treatment effects by assessing leaf measurements and SLA. I dealt with the non-independence of leaf measurements within species by using multivariate analyses of variance (MANOVA). *C. microchaeta* was the only species with a single leaf measurement, and so *C. microchaeta* and all SLA data were analyzed using ANOVAs. I dealt with the missing values following a method suggested by Quinn and Keough (2002) to deal with missing values in randomized block designs. The missing values for both leaf measurements and SLA were dealt with by substitution for the missing values. The population level averages, calculated as averages across all plots, were used for the substitutions as a conservative value that would not alter the population means. *C. microchaeta* leaf length data and SLA data were modeled using the *aov* function with Block as the first explanatory variable. All other leaf measurements were run using the *Manova* function in the 'car' package (Fox and Wiesburg 2011) with Block at the first explanatory variable. Normality of univariate data was assessed visually through QQ-plots (Crawley 2007). Multivariate normality of the data was assessed using

QQ-plots of chi-squared values against Mahalanobis distances (Burdenski 2000). Plotting of all data were done using both 'ggplot2' (Wickham 2009) and 'gplots' (Warnes 2010) packages.

3.3 RESULTS

3.3.1 Experimental Treatments

The solar powered warming treatment significantly increased the temperature in the warmed plots as compared to the control plots in both years. The warming treatment had the desired effect on soil temperature during the 2010 trial soil warming period, with a significant increase in both mean and minimum temperatures by close to 2°C (Table 3.3; Fig 3.2). Mean temperatures were increased by 2.1°C ± 0.6 (mean ± SE) and minimum temperatures by 2.0°C ± 0.52. Although the maximum temperatures were not significantly different between warming and control plots in 2010 this was mostly due to the greater variation in maximum temperatures, as the average maximum temperatures in the warming treatment were estimated at 2.1°C ± 0.97 above the controls. The warming treatment during the same time period in 2011 significantly increased the mean, minimum, and maximum temperatures as compared to the controls (Table 3.3; Fig 3.3), but it was not as effective at reaching the 2°C goal. The 2011 warming treatment increased mean temperatures by 1.4°C ± 0.26, minimum temperatures by 1.1°C ± 0.14, and maximum temperatures by 1.6°C ± 0.52. Similar to the previous year, maximum temperatures showed the greatest variation. Comparing the average temperatures of this time period between the two years shows that mean temperatures in the control plots were approximately 6.9°C ± 0.18 in 2011 while they were 10.8°C ± 0.43 in 2010. 2011 was much cooler during this time period than during 2010, and had much lower variation between plots. This could be the result of reduced solar radiation resulting in cooler soil

Table 3.3: Summary of mixed effects models with temporal pseudoreplication for warming treatment effects on mean, minimum, and maximum soil temperatures, using a first-order autoregressive autocorrelation structure (n = 12). The seven day sampling periods were treated as a random effect to account for temperatures collected from the same plot over time. Significant p-values are in bold font.

Year	Variable	t	P-value
2010	Mean Temperature	3.39	**0.007**
	Minimum Temperature	3.86	**0.003**
	Maximum Temperature	2.17	0.055
2011	Mean Temperature	5.64	**<0.001**
	Minimum Temperature	7.76	**<0.001**
	Maximum Temperature	3.15	**0.010**

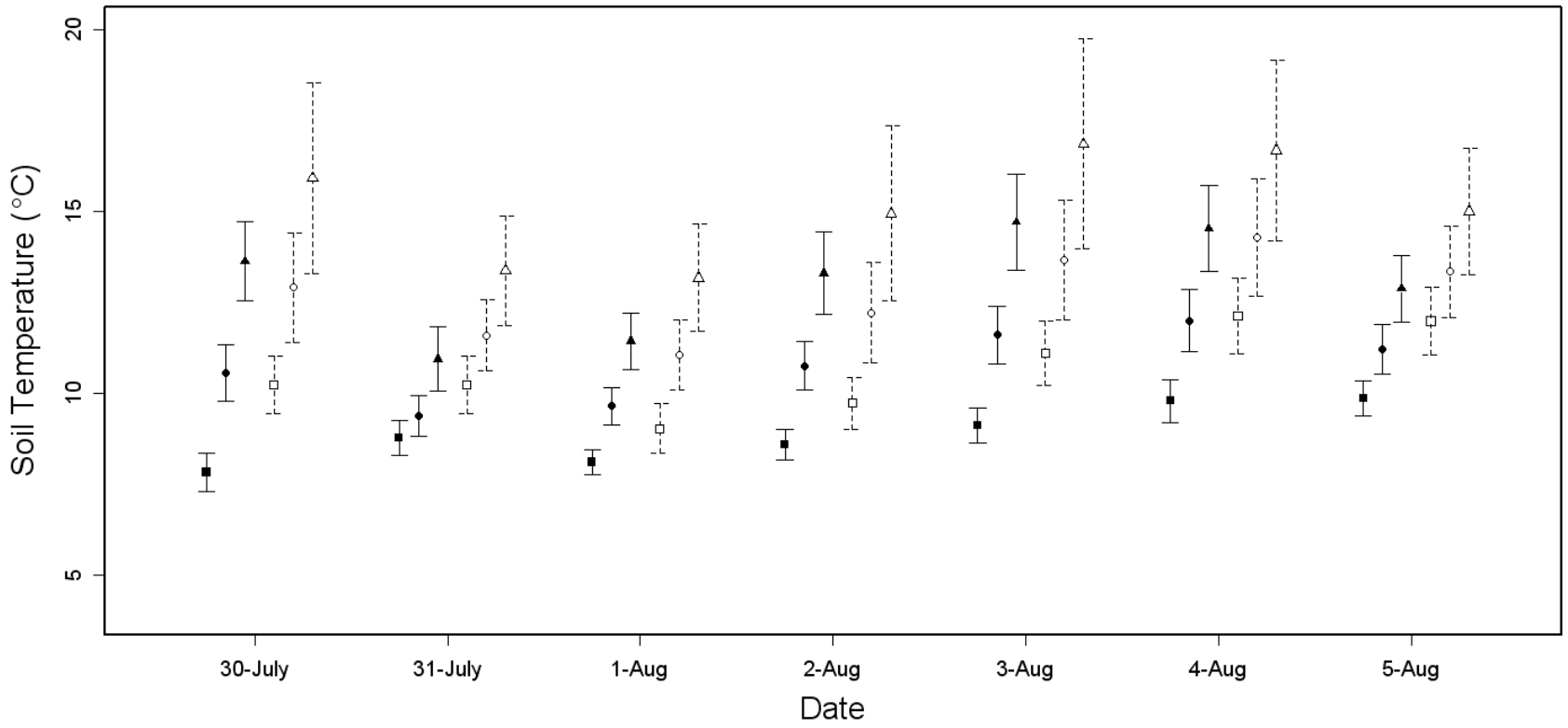

Figure 3.2: Average daily soil temperatures in control (solid symbols; n = 6 plots) and warmed plots (open symbols; n = 6 plots) from the trial warming period of 30 July to 5 August 2010. Solid and dashed whiskers indicate ± 1 standard deviation for control and warmed plots, respectively. Minimum temperatures are indicated by squares, mean temperatures by circles, and maximum temperatures by triangles. Minimum and maximum temperature points were shifted to the left and right, respectively, of the mean temperature points to avoid overlap of whiskers.

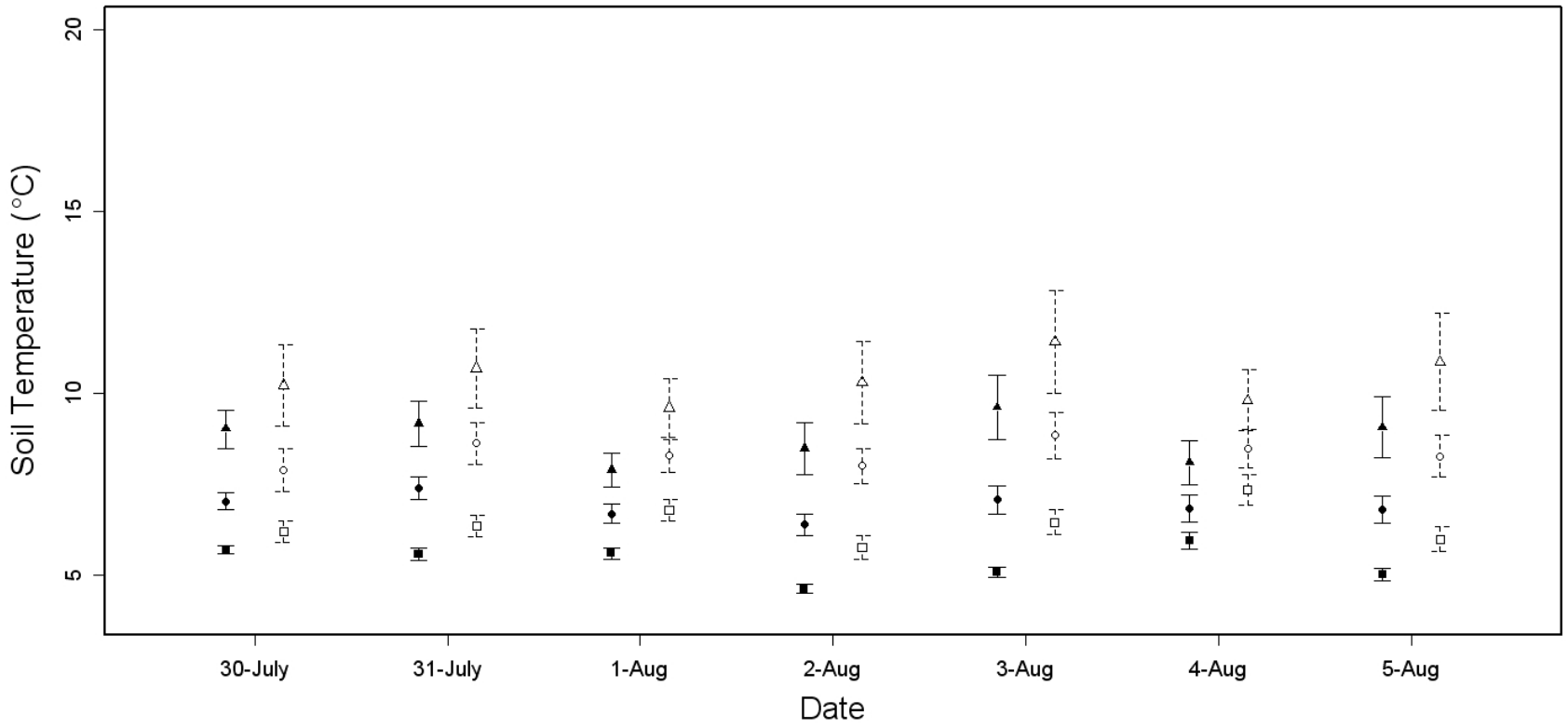

Figure 3.3: Average daily soil temperatures in control (solid symbols; n = 6 plots) and warmed plots (open symbols; n = 6 plots) from the first treatment year, 30 July to 5 August 2011. Solid and dashed whiskers indicate ± 1 standard deviation for control and warmed plots, respectively. Minimum temperatures are indicated by squares, mean temperatures by circles, and maximum temperatures by triangles.

temperatures and also in reduced solar power, which could explain the reduced warming effect in 2011.

Neither nitrate nor ammonium availability, as indexed by the ion resin beads, were significantly different among control and treated plots (Table 3.4; Fig 3.4). However, there did seem to be a trend of increased nitrate in fertilized plots. The trend of increased nitrate is likely associated with the fertilizer treatment as I observed no differences in nitrogen between treatments prior to fertilization. The pre-treatment soil samples did not show a difference in total nitrogen, nitrate, or ammonium pools in either the organic or mineral horizon when grouped by 2011 treatments (Fig 3.5). The organic horizon contained higher total nitrogen, ammonium, and nitrate as compared to the mineral horizon, and there were higher levels of ammonium in both the mineral and organic horizons as compared to nitrate. Further examination of the pre-treatment samples found no obvious differences between vegetation cover types, due to the high amounts of variation in both nitrogen values and sample sizes (Fig. 3.6). However, bare mineral soil, from frost boil areas, did appear to have lower amounts of total nitrogen and ammonium as compared to other vegetated samples. Inorganic nitrogen differed between all plots, with ammonium present in much higher levels than nitrate. The only exception to this was the bare soil plots, which appear to have similar levels of ammonium and nitrate.

3.3.2 Experimental Responses

Following a single season of treatment application there was little to no effect on plant productivity. The leaf measurements of one species, *Carex microchaeta* differed significantly between treatments (Tables 3.5 & 3.6). *C. microchaeta* showed a significant effect of all

treatment combinations on leaf length, with a stronger response to fertilization than warming (Fig 3.7a). The greatest increase in *C. microchaeta* leaf length was within plots with both fertilization and warming (Fig 3.7a). *C. microchaeta* SLA showed no response to fertilization (Fig 3.7b). *C. microchaeta* did show a significant effect of Block, with the 2 eastern most blocks having much lower values than the rest. This block effect may explain why there was a significant effect in all treatment combinations when the plotted data does not look very different (Fig 3.7a). While not significant, *Salix reticulata* showed a trend of increased SLA in fertilized plots as compared to controls (Table 3.6; Fig 3.8).

Table 3.4: Summary of mixed effects models of treatment effects on soil nitrogen following fertilization (n = 24). Block was included as a random effect and thus did not have a test statistic. Soil nitrogen measurements were from ion exchange resins sampling inorganic nitrogen, ammonium and nitrate, in g N per gram dry weight resin.

Nitrogen Measurement	Treatment	t-value	P-value
Nitrate	Fertilization	2.07	0.057
	Warming	-0.15	0.880
	Fert + Warming	0.52	0.611
Ammonium	Fertilization	0.00	0.999
	Warming	0.20	0.846
	Fert + Warming	-0.55	0.589

Table 3.5: Test results from the comparison of leaf measurements between treatments and their interactions. All tests included Block as the first factor, and were MANOVA's unless otherwise indicated (see Table 3.1 for leaf measurements; n = 24). All missing values (see Table 3.2) were replaced with the average measurement across all plots. Significant p-values are in bold font.

Species	Treatment	F	P-value
P. viviparum	Block	1.55	0.128
	Fertilization	0.26	0.853
	Warming	0.74	0.546
	Fert + Warming	0.60	0.626
L. arcticus	Block	1.66	0.095
	Fertilization	0.40	0.757
	Warming	0.80	0.515
	Fert + Warming	0.56	0.651
S. arctica	Block	0.43	0.918
	Fertilization	0.72	0.503
	Warming	0.62	0.552
	Fert + Warming	0.21	0.810
S. reticulata	Block	1.59	0.157
	Fertilization	0.65	0.538
	Warming	1.04	0.379
	Fert + Warming	0.33	0.728
D. octopetala	Block	0.80	0.627
	Fertilization	1.89	0.187
	Warming	2.15	0.153
	Fert + Warming	0.01	0.993
*C. microchaeta**	Block	5.82	**0.004**
	Fertilization	9.91	**0.007**
	Warming	5.80	**0.029**
	Fert + Warming	5.09	**0.039**

*ANOVA

Table 3.6: Test results from ANOVA's of specific leaf area (SLA) between treatments and their interactions, with Block as the first factor. No data was missing for *D. octopetala*, while missing values for the other species were replaced with the average measurement across all plots (n = 24; see Table 3.2 for missing samples).

Species	Treatment	F	P-value
L. arcticus	Block	0.71	0.626
	Fertilization	0.21	0.654
	Warming	0.93	0.351
	Fert + Warming	1.02	0.329
S. arctica	Block	0.57	0.723
	Fertilization	0.77	0.406
	Warming	1.28	0.290
	Fert + Warming	0.40	0.546
S. reticulata	Block	0.72	0.618
	Fertilization	4.34	0.055
	Warming	1.31	0.270
	Fert + Warming	0.65	0.433
D. octopetala	Block	0.44	0.813
	Fertilization	0.22	0.644
	Warming	3.20	0.094
	Fert + Warming	0.30	0.591
C. microchaeta	Block	0.44	0.808
	Fertilization	1.70	0.225
	Warming	0.01	0.908
	Fert + Warming	0.47	0.511

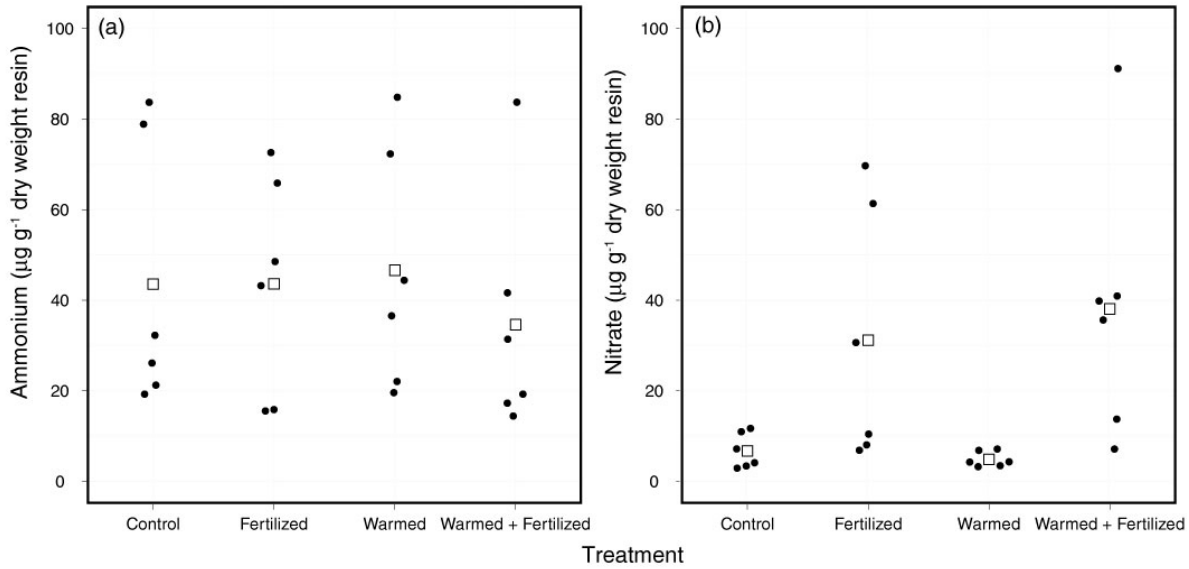

Figure 3.4: Inorganic nitrogen content, (a) ammonium and (b) nitrate, of ion exchange resin samples grouped by treatment (n = 6 plots per treatment). Mean values in each treatment combination are indicated by a hollow square. Data were 'jittered', moved slightly along the x-axis, to avoid overlap.

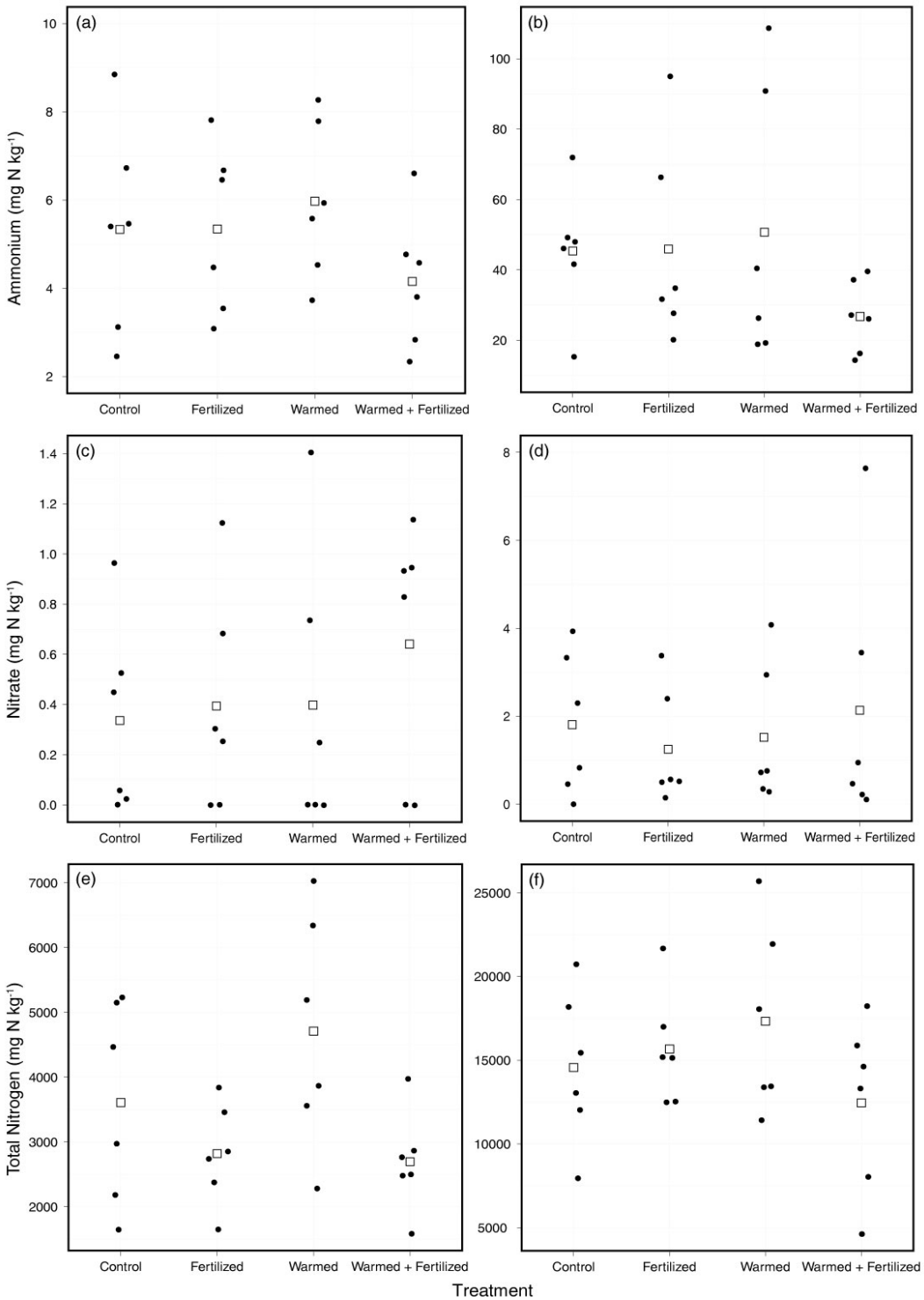

Figure 3.5: Nitrogen content, (a, b) ammonium, (c, d) nitrate, and (e, f) total nitrogen, of 2010 soil samples, grouped by treatment as applied in 2011 (n = 6 plots per treatment). The (a, c, e) mineral and (b, d, f) organic soil horizons are presented separately. Mean values in each treatment combination are indicated by a hollow square. Data were 'jittered', moved slightly along the x-axis, to avoid overlap. Note y-axis scales differ between mineral and organic layers for a given N pool.

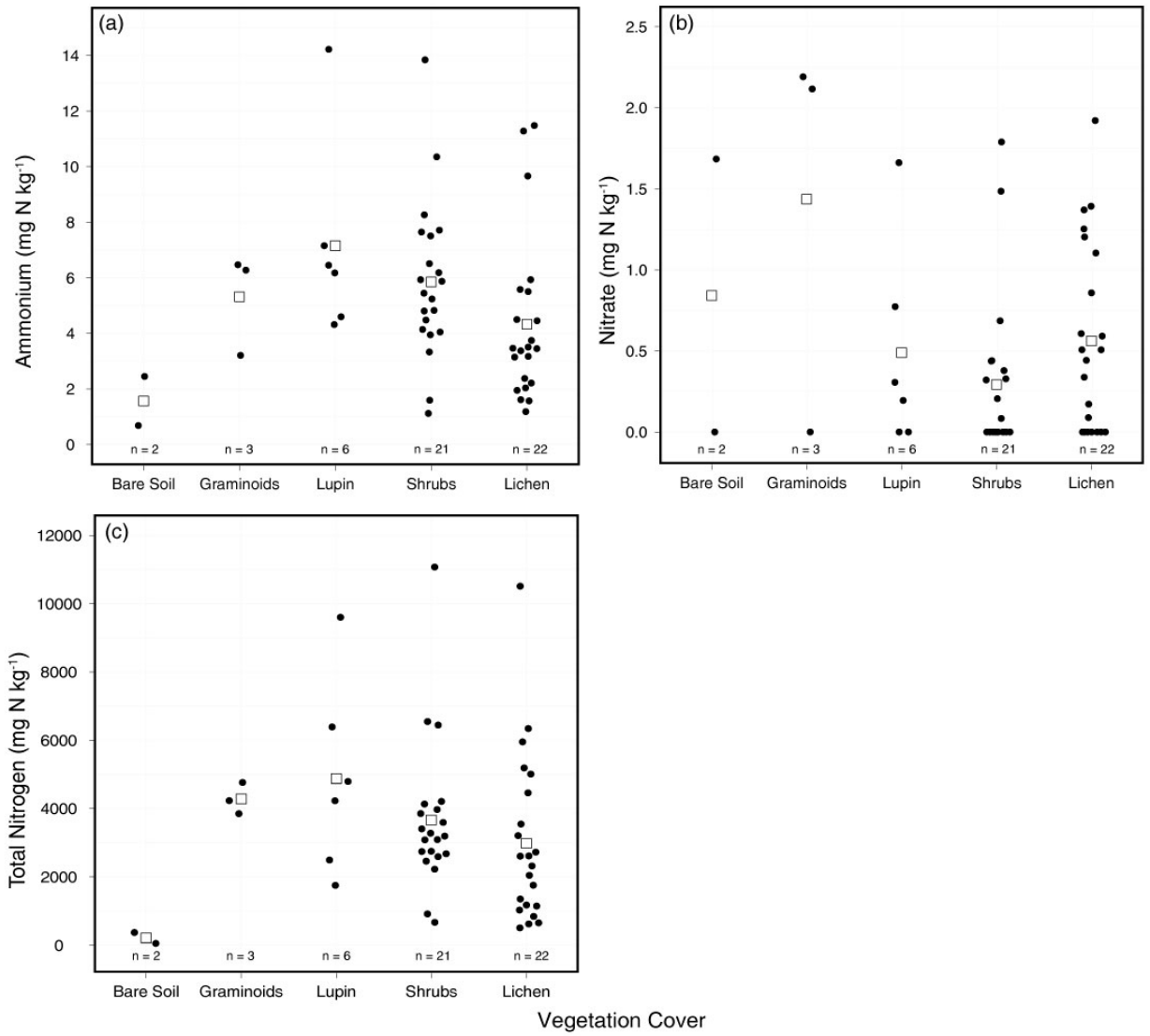

Figure 3.6: Nitrogen content, (a) ammonium, (b) nitrate, and (c) total nitrogen, of 2010 mineral horizon soil samples grouped by vegetative cover. Mean values in each treatment combination are indicated by a hollow square. Data were 'jittered', moved slightly along the x-axis, to avoid overlap. Note y-axis scales differ.

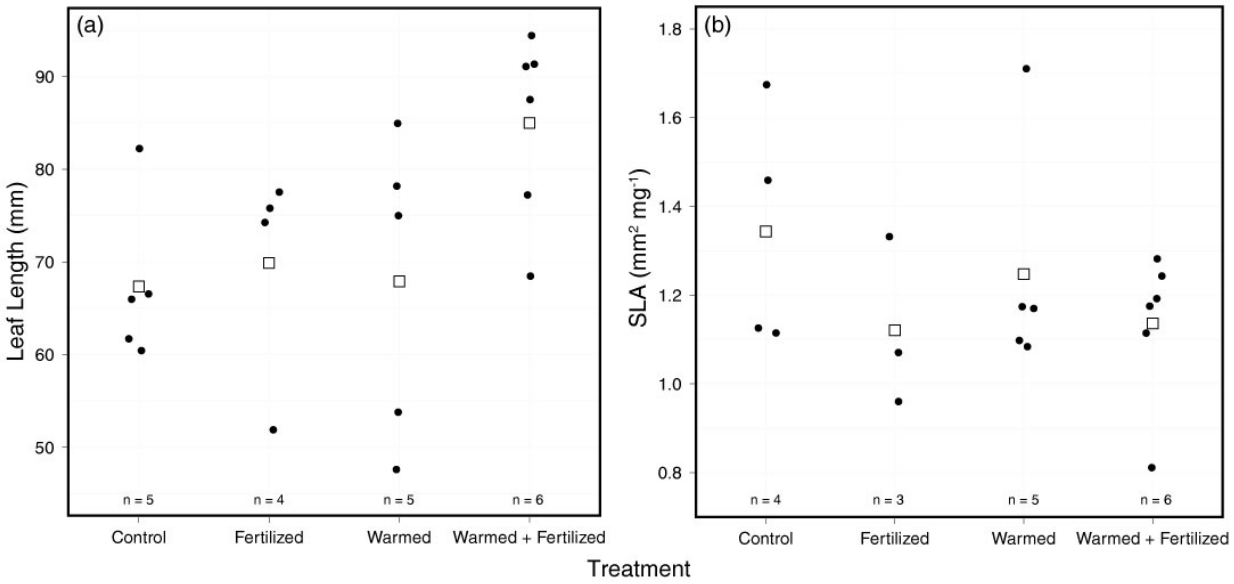

Figure 3.7: *Carex microchaeta* (a) leaf length and (b) specific leaf area grouped by treatment. Mean values in each treatment combination are indicated by a hollow square. Data were 'jittered', moved slightly along the x-axis, to avoid overlap.

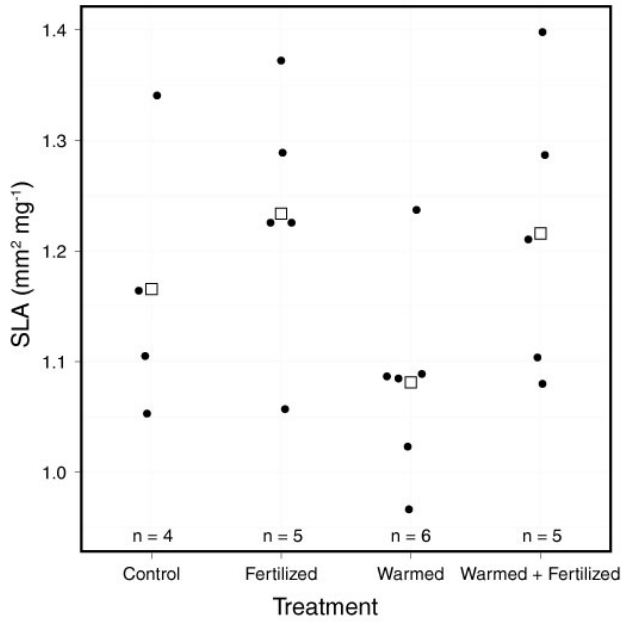

Figure 3.8: Specific leaf area index values for *Salix reticulata* grouped by treatment. Mean values in each treatment combination are indicated by a hollow square. Data were 'jittered', moved slightly along the x-axis, to avoid overlap.

3.4 DISCUSSION

3.4.1 Experimental Treatments

The solar-powered vertical heating probes proved to be an effective soil warming system. The trial soil warming period, from 30 July to 5 August 2010, increased temperatures in the warmed plots by approximately 2.0 to 2.1°C. This was very close to the aim of an increase of 2°C. Although the temperature data from 30 July to 5 August 2011, selected from the first year of warming treatment application, shows only approximately a 1.1 to 1.6°C increase in temperatures in warmed plots, they were significantly different from the control temperatures and the variation in the temperatures were decreased from the 2010 data. So while there might have been a greater response to the warming treatment if the aim of a 2°C increase had been met during the 2011 soil warming, there was still consistent warming across the treatment plots and thus the responses can be attributed to the warming treatment.

This active soil warming system has more consistent effects on soil temperature than passive systems. Passive warming systems, such as open top chambers, often have variable effects on the soil temperatures (Marion *et al.* 1997). As well, open top chambers can create many secondary effects on other environmental factors, such as wind speed, carbon dioxide concentrations, and moisture which can be system design or site specific (Marion *et al.* 1997). Soil moisture is often reduced with soil warming (Rustad *et al.* 2001), however the soil moisture at this site was highly variable between plots and not different between control and warmed plots (Johnstone *et al.* unpublished ms.). Heating cables are often associated with disturbance to both the plants and soil (Aronson and McNulty 2009), but the vertical placement of the probes was intended to decrease the root and soil microbe disturbance. While this system does

not simultaneously warm the air, as would be expected with climate change, it is still a useful tool for investigating the effects of climate change. This decoupling of soil and air warming can be used to differentiate between the effects of air and soil temperatures. As well, passive air warming systems, such as open top chambers, could be coupled with this soil warming system to more closely mimic climate change while more accurately reflecting the resulting temperature changes in both the air and soil. Active systems are rarely used in remote locations due to the limitations of accessing reliable power sources (Aronson and McNulty 2009), but this active system has proven to be reliable in a remote location with no access to the power grid. Johnstone *et al.* (unpublished ms.) provided a more in-depth description of the warming system and its uses in remote locations, which was beyond the scope of this thesis.

The application of 2 g nitrogen per fertilized plot did not result in a significant difference in either nitrate or ammonium available for resin uptake. This is to be expected after only a single fertilizer application. This lack of increased inorganic nitrogen with fertilization has been seen in other studies that used much higher fertilization rates than 2 g N m^{-2} (5.71 g NH_4NO_3 m^{-2}). One study found that after 2 years of fertilization at 25 g NH_4NO_3 m^{-2} there was no statistical difference in ammonium between treatments (Chapin and Shaver 1985), while another found that after 5 years of 10 g N m^{-2} fertilization only one of their two study sites showed an increase in ammonium in fertilized plots (Jonasson *et al.* 1999b). Longer term studies have seen increased ammonium and nitrate in fertilized plots, but only after 7 years (Chapin *et al.* 1995). Since the study area is strongly nitrogen limited, the inorganic nitrogen in the fertilizer may be taken up by plants, in both above- and belowground tissues, and immobilized by soil microbes

soon after fertilizer application. This would limit the amount of nitrogen that would reach the ion exchange resins 5 cm below the soil surface.

Although there was no statistically significant difference in inorganic nitrogen between the control and fertilized plots, nitrate did show a trend of increasing within fertilized plots while ammonium did not. This could be the result of ammonium being taken up at a faster rate than nitrate, which is consistent with the preferential uptake of ammonium by most plants (Nasholm *et al.* 2009), or due to the fact that nitrate is more mobile than ammonium (Chapin et al. 2011) and thus more nitrate was collected by the ion exchange resin bags While many plants do preferentially take up ammonium, there is increasing evidence that plants partition their nitrogen uptake (McKane *et al.* 2002, Sorensen *et al.* 2008a). This partitioning results in differing nitrogen contents in the soil under different species. While the difference in the 2010 nitrogen measurements taken under various vegetative covers was not statistically analyzed in this study, there did seem to be differences possible in ammonium and total nitrogen between plant cover types. As well, even within a single vegetation cover type there was a great deal of variation. This indicates that there is a high amount of micro-scale variation in nitrogen content, and multiple nitrogen measurements within a plot might be able to more accurately capture what is going on at the plot level.

The lack of a warming effect on nitrogen is not unexpected following a single season of warming. Many studies found little to no response of nitrogen after 2 (Jonasson *et al.* 1993), 5 (Jonasson *et al.* 1999b), 6 (Rinnan *et al.* 2007), and 16 (Lamb *et al.* 2011) years of warming, while others found increased nitrogen following 2 (Hartley *et al.* 1999) or 8 (Chapin *et al.* 1995) years of warming. The response of nitrogen to warming is quite variable, but a compilation of

warming studies has found that net nitrogen mineralization generally increases with warming after 2 to 9 years of treatment (Rustad *et al.* 2001). While my study did not assess nitrogen mineralization, it can still be expected that resin available inorganic nitrogen would not be altered following a single season of warming. One study looking at ion exchange resin absorbed nitrogen found no difference between nitrate or ammonium due to warming treatments after 3.5 years (Hobbie and Chapin 1998), while another found that after 8 years of treatment application nitrate increased with both the warming and the warming + fertilization treatment (Chapin *et al.* 1995). While warming might cause changes to nitrogen pools and cycling rates following a single season, the nitrogen limitation of both the plants and microbes could ensure that much of the newly available nitrogen would be quickly assimilated and thus not reach the ion exchange resins. This could be assessed by looking at plant response to warming.

3.4.2 Experimental Responses

Carex microchaeta leaf length showed a response to all treatment combinations, with a stronger response to fertilization than to warming. The stronger response to fertilization is consistent with previous studies that found plant biomass to be more strongly affected by fertilizer than any other treatment (van Wijk *et al.* 2003). It also supports the view that indirect effects of temperature on nutrients are more important than low temperatures alone for plant growth in arctic and alpine tundra (e.g., Chapin *et al.* 1995, Hobbie and Chapin 1998, Brooker and van der Wal 2003). The initial response of a graminoid to fertilization, and no other species, in this study is consistent with other studies that found graminoids to be the first functional group to respond to nitrogen addition in both arctic and alpine tundra (e.g., Press *et al.* 1998, Bowman *et al.* 2006, Haugwitz and Michelsen 2011). Graminoids often continue to show

positive growth responses to long term fertilization, but the magnitude generally decreases and other species start to respond more strongly (e.g., Shaver *et al.* 2001, Bowman *et al.* 2006, Haugwitz and Michelsen 2011).

While graminoids appear to be more responsive to nitrogen additions, they have also been found to show initial responses to increased temperatures as well (Walker *et al.* 2006, Elmendorf *et al.* 2012a). *C. microchaeta* showed the greatest leaf length response in plots that were both warmed and fertilized. The different strength responses to the treatments may be a result of increased temperatures reducing the energy required for internal processes, such as uptake of nitrogen (Nasholm *et al.* 2009). The greater response to the interaction of fertilization and temperature is consistent with there being an additive effect of these treatments, where fertilization increased available nitrogen and increased temperatures allows for more nitrogen uptake.

There was no significant effect of the experimental treatments on SLA of any species. However, the SLA of *S. reticulata* suggested a weak response to fertilization, a slight increase in SLA. Since there was no concurrent difference in *S. reticulata* leaf measurements, and SLA is the one-sided area of a leaf divided by its dry mass, the change in SLA must be a response of leaf thickness. Increasing SLA with no change in leaf dimensions indicates that the leaves were getting thinner. Specific leaf area is generally positively related to the relative growth rate, greater root nitrogen uptake, higher leaf nitrogen concentrations, and increased photosynthesis (e.g., Cornelissen *et al.* 2003, Meziane and Shipley 2001, Osone *et al.* 2008). As well, lower SLA values have been associated with plants in resource stressed environments

while higher SLA values are found in resource rich environments (Cornelissen *et al.* 2003). This change in SLA with resource availability could explain the increase in SLA with fertilization.

It is surprising that while *C. microchaeta* showed a significant leaf length response to all treatments it did not show a SLA response. Since SLA is based on leaf dimensions, a change in leaf length would generally result in a changed SLA value unless leaf weight changed concordantly. The strongest response in *C. microchaeta* leaf length was in response to fertilization, and it would be expected that a similar response would be found in SLA due to the strong relationship between nitrogen uptake and SLA. Changes in SLA have not only been associated with nitrogen assimilation, but also with changes in temperatures (Atkin *et al.* 2006). Increases in both temperature and nutrient availability are associated with increased leaf expansion, but decreased leaf thickness (Terry *et al.* 1983). This would cause an increase in SLA, which is consistent with SLA having a positive relationship with relative growth rate (e.g., Cornelissen *et al.* 2003, Shipley 2006, Osone *et al.* 2008). The changes in SLA with temperature are often associated with faster growing species; which, considering that *C. microchaeta* was the only species to respond to the experimental treatments and that graminoids often show initial responses to experimental manipulations, it would be expected that SLA would change also. The lack of a SLA response could be a result of increased leaf elongation without an associated change in leaf thickness. However, the data suggests that SLA of *C. microchaeta* is actually decreasing with increased temperature and nitrogen. The most likely reason that SLA of *C. microchaeta* was not significantly different, despite the fact that leaf length was, and that it appears to have lower SLA with the treatments is due to the high number of missing data. In particular the lack of a fertilization response could be due to that most of the missing values of

C. microchaeta were in the fertilized plots. This would reduce the power of the analyses to detect differences in treatments, particularly for SLA, which had missing values for half of the fertilized plots. In fact the results of all of the species which had missing values should be considered as approximate responses due to the missing values within such a low number of replicates. The replacement of missing values with the average measurement across all plots, while not affecting the overall mean, did reduce the effective sample size and thus the power of the experiment to detect true differences between treatments.

Plant productivity measures at this study site were restricted to ones that reduced destructive sampling, due to the long-term nature of the study. The leaf dimensions measured on the species in this study were non-destructive measurements of number of leaves, leaf widths, lengths, and petiole lengths. A study at a nearby site examined non-destructive leaf dimension measurements for their relationship to leaf area and leaf mass (Pieper *et al.* 2011). They assessed many of the same species that were examined in this study, and found that the leaf dimension measurements were strongly related to leaf area and leaf mass, and thus gave a good indicator of plant growth. Specific leaf area is a closely related measure of leaf size, but also takes into account the mass of the leaf; the one-sided area of a leaf divided by its dry mass. Specific leaf area is generally positively related to the relative growth rate of a species (e.g., Cornelissen *et al.* 2003, Shipley 2006, Osone *et al.* 2008) and as such is a good proxy for plant productivity.

3.4.3 Future Directions

Continuous monitoring of plant productivity responses at this site could allow for a more detailed look at how long it takes for each species start to respond to climate change, and how

those responses change over time. I expect plant growth responses to nitrogen will continue to increase in the first few years of the experiment and deciduous shrubs to show a response following graminoids. *Lupinus arcticus* may be the last species to show a fertilization response due to the fact that the species is a nitrogen-fixing legume. I expect responses to soil temperature manipulations will take longer to emerge, but will follow the same pattern of species response as nitrogen, first graminoids followed by deciduous shrubs. This study focused on aboveground changes to plant productivity due to fertilization and warming; however, including changes in belowground plant growth and root production would give a better idea on how species respond to a changing climate, at the whole plant level. Although changes in plant productivity are likely to occur before changes in community composition, changes in reproductive output are also likely. Changes in arctic and alpine plant productivity are generally associated with inital responses, while reproductive effort often increases with long-term manipulations (Arft *et al.* 1999), thus continuous monitoring of reproductive aspects is also important at this site.

3.4.4 Conclusion

I found that following a single season of treatment application, few species showed plant productivity responses to experimental warming or nitrogen fertilization. *C. microchaeta* was the only species that showed a leaf measurement response to the treatments, with increased leaf length with all treatments. The initial response of a graminoid to the warming treatment has been commonly found in air warming experiments (Elmendorf *et al.* 2012a), thus the initial responses of plant growth to soil warming were consistent with air warming experiments. In addition, I found that *C. microchaeta* showed the strongest response to the interaction of

warming and fertilization and had a greater response to fertilization than warming, and *S. reticulata* showed a slight increase in SLA with fertilization. This could indicate that this site is more nitrogen limited than temperature limited, or that changes in leaf traits with increased soil temperatures take longer to appear than those due to increased nitrogen, such as the indirect effects of temperature on nitrogen. The results of this study supports previous studies that found nitrogen to be the most limiting factor at arctic and alpine tundra sites (e.g., Shaver and Chapin 1980, Nadelhoffer *et al.* 1992, Atkin 1996). The hypothesized increase of nitrogen pools due to soil warming was not seen after one season of continuous warming, which is consistent with observations from other fertilization studies (Chapin and Shaver 1985, Jonasson *et al.* 1999b), and is likely due to plants or microbes taking up the available nitrogen. This study indicates that the initial effects of fertilization are stronger than the initial effects of soil warming when soil temperature was modified directly using a solar-powered soil heating system.

4.0 CONCLUSIONS

4.1 PRODUCTIVITY RESPONSES TO A CHANGING CLIMATE

The results of the vegetation gradient study indicate that the tall shrub habitat had different relationships with the measured environmental variables as compared to the other vegetation types present: low shrubs, wind-swept ridge tops, late-lying snow beds, and frost boils. I found that when all vegetation types were included in the analyses and when tall shrubs were removed plant productivity was most strongly related to total soil nitrogen, followed by soil moisture. The productivity of tall shrub habitats was only, and quite strongly, related to mean soil temperature. The tall shrub plots had values of environmental variables that were quite similar to the other vegetation types, but they had much higher levels of plant productivity.

The experimental nitrogen fertilization and soil warming study found similar responses to the treatments as found in other experimental studies in arctic and alpine tundra. The single graminoid assessed in the experimental study, *Carex microchaeta*, was the only species to show a significant growth response to the treatments. I found that *C. microchaeta* leaf length showed a significant response to all treatment combinations with the strongest response to the warming + fertilization treatments, followed by fertilization and then warming. The initial response of graminoids to both nitrogen fertilization and warmer temperatures is consistent with other studies that found graminoids to be initially the most responsive to environmental manipulations (e.g., Press *et al.* 1998, Walker *et al.* 2006, Haugwitz and Michelsen 2011). The strongest response of *C. microchaeta* to the warming + fertilization treatment indicates that there is an additive effect of the treatments, perhaps due to increased temperatures allowing for better utilization of the increased nitrogen (Nasholm *et al.* 2009). The stronger response of *C. microchaeta* to fertilization than warming is consistent with other studies that found

nitrogen to be the most limiting factor in arctic and alpine tundra (e.g., Shaver and Chapin 1980, Nadelhoffer *et al.* 1992, Atkin 1996).

Nitrogen fixation is an important source of external nitrogen input into Arctic ecosystems, mostly through cyanobacteria in biological soil crusts (Chapin and Bledsoe 1992). The presence of plants with nitrogen-fixing symbionts can be variable across the arctic, with the same species showing symbioses with nitrogen-fixing bacteria at one site and not at another (Chapin and Bledsoe 1992). Nitrogen-fixing plants have a competitive advantage over other non-fixing plants in sites with low nitrogen availability (Vitousek and Howarth 1991). Nitrogen-fixing plants could colonize these areas, and over time soil nitrogen levels would rise and other plants would colonize due to the decomposition of the nitrogen-fixing plants (Chapin and Bledsoe 1992). The process of fixing atmospheric nitrogen is more energetically expensive than taking up inorganic nitrogen from the soil (Gutschick 1981, Vitousek and Howarth 1991). Thus, nitrogen-fixing plants, such as the species *Lupinus arcticus* included in the experimental study, may not be nitrogen limited due to their ability to fix nitrogen. However, they may show a response to increased available soil nitrogen by including an energetically less expensive source of nitrogen. *L. arcticus* showed no response to a single season of fertilization in the experimental study, but the response of a nitrogen-fixing plant to increased nitrogen may take longer to appear than in other species that are currently nitrogen limited.

Combining the results of the gradient and experimental studies can help to more accurately predict the effects of climate change at this site. Short term changes to plant growth with climate change are likely to result in the increase in graminoid growth, with the strongest growth response resulting from increased nitrogen availability. Long term changes are more

difficult to predict, due to the individualistic responses of different species to changing environmental conditions found in both this study and others (e.g., Chapin and Shaver 1985, Klanderud 2008, Pieper *et al.* 2011). Increased plant productivity in both the short and long term is most likely going to be associated with increased nitrogen availability, since both the gradient and experimental study results are consistent with nitrogen being a limiting factor for plant growth. While causality cannot be inferred from the gradient study, the strong relationship of soil moisture with both plant productivity and soil nitrogen could indicate that changes in precipitation may be an important determinant of future plant productivity at this alpine site. However, the much higher productivity present in tall shrub habitats and their strong correlation with mean soil temperature leads me to hypothesize that tall shrubs will show the greatest growth response to increased soil temperatures over the long term.

The expansion of shrub tundra has already been observed across both arctic and alpine environments (e.g., Tape et al. 2006, Hallinger et al. 2010, Myers-Smith et al. 2011). However, other long-term studies have found cases of graminoids and deciduous shrubs experiencing similar increases (van Wijk et al. 2003, McManus et al. 2012), and in the experimental study a graminoid was the only species to respond to fertilization and warming treatments. Thus the ability to take greater advantage of changing climates than other vegetation may be site specific. In the gradient study plots there were no vegetation types that were dominated by graminoids, and the highest number of graminoids was found in the tall shrub plots. This could have been due to the moderated environment present within a tall shrub canopy being better for graminoid growth than in the more exposed plots. Regardless, the initial response of graminoids in the experimental study coupled with the greater tall shrub productivity in the

gradient study indicate that while graminoids may be able to respond the fastest to changing climates, tall shrubs have the ability to show a greater growth response.

4.2 FUTURE RESEARCH

From my findings in the gradient study I would suggest two modifications to the study design. The use of a sampling method that could differentiate organic and inorganic nitrogen or measuring nitrogen cycling rates would improve the ability to detect more subtle differences between plots. As well, I would suggest sampling a vegetation gradient using a transect sampling system, where plots were set up along transects from the ridge top down the slope. This system would have captured more variation in vegetation than the five pre-determined vegetation types used in this study.

The gradient study portion of this research has given a good basis for understanding the current spatial relationships between environmental factors and plant productivity at this site. Further landscape scale studies could be done to capture how these relationships vary across time. In particular, a similar study using environmental measures taken immediately after snow melt could determine what environmental factors during the early growing season most influence peak plant productivity. For example, early in the growing season soil moisture may not limit plant growth or soil nitrogen due to snow melt. This could result in early growing season soil moisture having a weaker relationship with plant productivity than soil moisture later in the season. Determining what environmental relationships are present at different times of year could also lead to better interpretations of the experimental results, by understanding when plants are most sensitive to a changing climate.

The experimental study reported here is a part of a long-term collaborative project, of which I focused on the initial impacts of soil warming and increased nitrogen availability on native plant productivity. The results are from the first year of environmental manipulations, and as such show the responses of only those species that are especially sensitive to climate change and have the ability to quickly alter their growth response. Yearly monitoring of native plant productivity would increase our understanding of the time scale over which different species respond to climate change, and how those responses change over time. In addition to productivity, reproductive effort is also expected to change with a changing climate. Concurrent monitoring of plant reproduction could lend insight into how different species may change in abundance, whether it is through vegetative expansion or an increase in sexual reproduction.

This experimental study was aimed at understanding how soil processes affect tundra vegetation, particularly looking at soil temperature effects on soil nitrogen. The strong relationships found in the gradient study of soil moisture with plant productivity, soil nitrogen and soil temperature would indicate that an additional watering treatment would be useful at this site to determine how changing precipitation regimes might affect tundra vegetation. Additionally, many studies have focused on a single warming method, air or soil, but climate change will include warming of both air and soil concurrently. An extension of this experimental study, with air warming coupled with the solar powered soil warming, would give additional information on the potential effects of climate change.

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6.0 APPENDIX A: GRADIENT STUDY DATA

Table A.1: Summary of gradient study plot level topographic information, including the vegetation type, locations of the plots, and topographic information. Each plot was named according to the sampling area (S1 to S4), the vegetation type (H1 to H5) and the replicate number (1 to 3). Dashes indicate missing data.

Study Area	Vegetation Type	Plot ID	Latitude	Longitude	Slope (degrees)	Aspect (degrees)	Elevation (m asl)
1	Ridge Top	S1H1-1	60°33'12.3"	135°07'45.2"	13	285.6	1548
		S1H1-2	60°33'12.3"	135°07'46.1"	12	334.3	1542
		S1H1-3	60°33'12.0"	135°07'47.0"	14	180.3	1540
	Low Shrub	S1H2-1	60°33'10.0"	135°07'48.7"	10	129.2	1531
		S1H2-2	60°33'10.0"	135°07'46.8"	17	62.4	1530
		S1H2-3	60°33'09.8"	135°07'45.5"	17	224.3	1525
	Tall Shrub	S1H3-1	60°33'08.6"	135°07'42.0"	12	27.3	1508
		S1H3-2	60°33'09.9"	135°07'45.1"	15	255.3	1528
		S1H3-3	60°33'11.2"	135°07'43.9"	11	238.7	1541
	Snowbed	S1H4-1	60°33'09.6"	135°07'41.4"	10	277.9	1523
		S1H4-2	60°33'08.5"	135°07'44.0"	8	304.6	1523
		S1H4-3	60°33'07.7"	135°07'45.1"	8	341.3	1515
	Frostboil	S1H5-1	60°33'08.4"	135°07'45.6"	4	24.2	1516
		S1H5-2	60°33'11.5"	135°07'46.9"	9	297.1	1548
		S1H5-3	60°33'12.1"	135°07'45.6"	13	334.3	1549
2	Ridge Top	S2H1-1	60°33'12.9"	135°07'48.2"	1	170.8	1552
		S2H1-2	60°33'13.2"	135°07'44.9"	8	117.4	1547
		S2H1-3	60°33'12.9"	135°07'45.2"	0	187.9	1549
	Low Shrub	S2H2-1	60°33'13.7"	135°07'48.2"	3	172.6	1541
		S2H2-2	60°33'14.7"	135°07'48.7"	13	352.1	1538
		S2H2-3	60°33'16.4"	135°07'48.4"	11	45.6	1525
	Tall Shrub	S2H3-1	60°33'14.5"	135°07'47.0"	17	25.2	1539
		S2H3-2	60°33'14.2"	135°07'47.7"	10	61.0	1541
		S2H3-3	60°33'16.2"	135°07'48.7"	8	45.6	1526
	Snowbed	S2H4-1	60°33'14.0"	135°07'46.4"	11	358.8	1543
		S2H4-2	60°33'15.1"	135°07'46.3"	9	85.3	1533
		S2H4-3	60°33'15.4"	135°07'48.6"	19	41.6	1531
	Frostboil	S2H5-1	60°33'14.3"	135°07'46.3"	2	358.8	1541
		S2H5-2	60°33'14.4"	135°07'47.4"	3	25.2	1542
		S2H5-3	60°33'13.9"	135°07'48.7"	0	252.0	1542

Study Area	Vegetation Type	Plot ID	Latitude	Longitude	Slope (degrees)	Aspect (degrees)	Elevation (m asl)
3	Ridge Top	S3H1-1	60°34'01.5"	135°08'38.2"	12	171.1	1582
		S3H1-2	60°34'00.4"	135°08'36.8"	5	146.8	1576
		S3H1-3	60°34'01.2"	135°08'35.0"	1	174.7	1579
	Low Shrub	S3H2-1	60°33'57.8"	135°08'37.7"	1	20.9	1568
		S3H2-2	60°33'57.6"	135°08'37.6"	3	20.9	1568
		S3H2-3	60°33'58.1"	135°08'33.7"	1	355.0	1569
	Tall Shrub	S3H3-1	60°33'56.4"	135°08'34.3"	15	339.9	1563
		S3H3-2	60°33'55.7"	135°08'34.8"	3	347.9	1559
		S3H3-3	60°33'55.5"	135°08'36.4"	2	13.6	1563
	Snowbed	S3H4-1	60°33'56.6"	135°08'31.8"	9	79.1	1569
		S3H4-2	60°33'58.1"	135°08'30.4"	7	25.9	1556
		S3H4-3	60°33'58.4"	135°08'35.0"	4	63.2	1560
	Frostboil	S3H5-1	60°33'57.8"	135°08'35.2"	0	52.6	1564
		S3H5-2	60°33'56.9"	135°08'35.0"	-	38.1	1568
		S3H5-3	60°33'57.2"	135°08'33.6"	2	13.8	1569
4	Ridge Top	S4H1-1	60°34'04.8"	135°08'38.2"	3	197.0	1576
		S4H1-2	60°34'04.2"	135°08'38.0"	8	197.0	1578
		S4H1-3	60°34'04.8"	135°08'39.2"	8	193.5	1580
	Low Shrub	S4H2-1	60°34'08.5"	135°08'40.6"	12	44.0	1549
		S4H2-2	60°34'07.2"	135°08'42.2"	15	189.7	1567
		S4H2-3	60°34'08.1"	135°08'37.3"	22	162.6	1584
	Tall Shrub	S4H3-1	60°34'07.7"	135°08'42.6"	17	218.9	1555
		S4H3-2	60°34'07.9"	135°08'38.7"	17	315.8	1562
		S4H3-3	60°34'08.0"	135°08'36.3"	2	224.5	1561
	Snowbed	S4H4-1	60°34'05.9"	135°08'36.6"	32	261.8	1569
		S4H4-2	60°34'08.4"	135°08'38.0"	13	169.0	1550
		S4H4-3	60°34'08.4"	135°08'39.7"	9	0.7	1549
	Frostboil	S4H5-1	60°34'08.4"	135°08'40.8"	2	44.0	1550
		S4H5-2	60°34'06.9"	135°08'38.6"	8	105.6	1570
		S4H5-3	60°34'05.9"	135°08'38.0"	6	136.0	1575

Table A.2: Summary of gradient study soil temperature, total nitrogen, snow depth, and soil moisture data. Each plot was named according to the sampling area (S1 to S4), the vegetation type (H1 to H5) and the replicate number (1 to 3). See methods section 2.2.3 and 2.2.4 for more information regarding sample collection. Abbreviation: coefficient of variation (CV). Dashes indicate missing data.

Plot ID	Soil Temperature		Total N	Snow Depth	Soil Moisture
	Mean (°C)	CV	(mg N/kg soil)	(cm)	(% dry weight)
S1H1-1	-2.24	0.0307	11978	20	25.00
S1H1-2	-2.83	0.0350	8851.2	2	-
S1H1-3	-2.41	0.0308	9953.7	5	38.14
S1H2-1	-1.57	0.0256	10691	20	38.39
S1H2-2	-0.77	0.0240	14705	20	59.72
S1H2-3	-1.58	0.0235	21890	20	169.76
S1H3-1	-0.66	0.0167	5366.2	-	71.39
S1H3-2	-1.28	0.0200	24202	42	147.56
S1H3-3	-2.20	0.0230	19088	35	34.39
S1H4-1	0.84	0.0151	4339.7	-	61.80
S1H4-2	0.54	0.0100	8448.4	-	58.59
S1H4-3	0.96	0.0171	10856	-	89.29
S1H5-1	1.11	0.0193	3435.5	-	28.49
S1H5-2	-	-	846.4	7	9.71
S1H5-3	-1.83	0.0321	3107.6	25	18.53
S2H1-1	-3.08	0.0340	12537	2	31.77
S2H1-2	-	-	13426	15	36.39
S2H1-3	-3.35	0.0353	8868.8	1	17.70
S2H2-1	-1.43	0.0197	2580.4	35	22.78
S2H2-2	-3.01	0.0258	7186	-	18.43
S2H2-3	-1.87	0.0223	3579.7	30	60.13
S2H3-1	-1.26	0.0173	11646	70	34.85
S2H3-2	-2.54	0.0204	4665.2	50	45.84
S2H3-3	-1.66	0.0153	8407.7	65	41.16
S2H4-1	-1.11	0.0150	7802	100	55.98
S2H4-2	-0.68	0.0085	16058	-	53.54
S2H4-3	-0.57	0.0135	15111	28	143.95
S2H5-1	-1.28	0.0236	3432.1	61	23.35
S2H5-2	-2.05	0.0268	1969.6	-	38.10
S2H5-3	-2.57	0.0281	1044.4	30	10.43

Plot ID	Soil Temperature		Total N	Snow Depth	Soil Moisture
	Mean (°C)	CV	(mg N/kg soil)	(cm)	(% dry weight)
S3H1-1	-1.95	0.0315	10420	-	27.69
S3H1-2	-1.79	0.0288	4786.5	-	21.23
S3H1-3	-	-	12179	20	24.65
S3H2-1	-1.58	0.0228	12078	33	57.36
S3H2-2	-	-	7406.1	25	18.13
S3H2-3	-1.21	0.0186	4997.9	55	56.95
S3H3-1	-1.39	0.0166	10051	28	31.59
S3H3-2	-1.27	0.0138	18548	51	103.92
S3H3-3	-1.36	0.0137	8967.5	40	52.80
S3H4-1	-0.02	0.0113	21628	-	229.63
S3H4-2	-	-	9776	-	24.70
S3H4-3	-0.01	0.0149	7000.5	100	29.54
S3H5-1	-0.20	0.0191	613.3		16.12
S3H5-2	-0.76	0.0221	640.5	35	12.48
S3H5-3	-0.11	0.0195	611	-	11.82
S4H1-1	-3.42	0.0294	9431.4	19	34.82
S4H1-2	-2.42	0.0279	8615.3	22	34.20
S4H1-3	-3.44	0.0327	8718.1	19	24.14
S4H2-1	-3.13	0.0262	5733.5	28	17.61
S4H2-2	-2.28	0.0219	2470.8	-	18.72
S4H2-3	-2.90	0.0199	14515	49	73.64
S4H3-1	-2.23	0.0193	11796	52	40.43
S4H3-2	-2.76	0.0214	18023	35	22.00
S4H3-3	-2.30	0.0220	5314.7	70	78.46
S4H4-1	-2.07	0.0209	7293.8	92	35.67
S4H4-2	-1.39	0.0177	10212	52	105.25
S4H4-3	-0.54	0.0158	11664	-	72.60
S4H5-1	-2.92	0.0311	3916.7	52	19.67
S4H5-2	-2.87	0.0283	1203.7	-	27.22
S4H5-3	-1.70	0.0254	3511.3	80	14.89

Table A.3: Summary of gradient study plant productivity measurements. Each plot was named according to the sampling area (S1 to S4), the vegetation type (H1 to H5) and the replicate number (1 to 3). See methods section 2.2.3 and 2.2.4 for more information regarding sample collection. Abbreviations: canopy height (CH), leaf area index (LAI), total vascular (TV), graminoids (Gram), forbs (Forb), deciduous shrubs (DS), evergreen shrubs (ES), and bare soil (Bare).

Plot ID	CH (cm)	LAI	Point Intercept Hits					Percent Cover (%)								
			TV	Gram	Forb	DS	ES	TV	Gram	Forb	DS	ES	Rock	Bare	Litter	Lichen
S1H1-1	3.6	0.21	125	31	9	0	85	61	5	6	0	50	4	1	20	11
S1H1-2	1	0.07	76	12	14	0	50	48	6	7	0	35	13	0	15	25
S1H1-3	3.2	0.07	104	8	27	0	69	56	6	10	0	40	3	0	20	20
S1H2-1	1.8	0.04	39	4	19	0	16	37	2	10	0	25	2	2	17	40
S1H2-2	7.2	0.34	113	47	7	5	54	48	15	4	5	24	3	3	25	22
S1H2-3	3.2	0.25	148	25	16	52	55	65	5	10	25	25	0.5	2	25	10
S1H3-1	40	3.09	342	23	3	302	14	85	3	1	80	1	0	0	15	0
S1H3-2	42.8	1.69	162	8	14	136	4	72	3	7	60	2	0	0	20	10
S1H3-3	29.6	2.37	326	97	7	222	0	69	7	2	60	0	0.5	0	25	1
S1H4-1	8	1.42	75	10	6	9	50	55	5	7	8	35	1	0	30	12
S1H4-2	9.4	1.28	101	10	3	34	54	59	5	4	25	25	0	0	35	5
S1H4-3	10.4	0.25	68	40	22	5	1	33.5	12	20	1	0.5	0	0	15	55
S1H5-1	1.4	0.25	99	38	12	49	0	37.1	7	5	25	0.1	6	30	15	12
S1H5-2	1	0.05	46	4	0	0	42	33	4	1	0	28	30	20	10	7
S1H5-3	0.2	0.26	40	3	6	25	6	24	4	7	10	3	45	2	6	30
S2H1-1	1	0.02	99	26	12	0	61	66	6	5	0	55	10	0	3	20
S2H1-2	1.2	0.03	64	8	5	0	51	32.1	5	2	0.1	25	0.1	0	4	60
S2H1-3	1.2	0.04	73	16	17	0	40	43	5	3	0	35	20	0	3	30
S2H2-1	0.2	0.07	58	4	0	52	2	35.5	4	0.5	30	1	1	0	3	60
S2H2-2	1.4	0.03	55	0	0	38	17	41.5	1	0.5	30	10	0	0	4	50
S2H2-3	1.4	0.05	27	3	2	9	13	19	3	2	10	4	2	0	2	75
S2H3-1	22.2	2.78	264	56	0	201	7	77	15	0	60	2	0	0	12	10
S2H3-2	18	1.56	242	23	0	217	2	60.1	4	0.1	55	1	0	0	25	15
S2H3-3	20.4	2.57	276	37	0	217	22	75	7	0	65	3	0	0	15	10

Plot ID	CH (cm)	LAI	Point Intercept Hits					Percent Cover (%)								
			TV	Gram	Forb	DS	ES	TV	Gram	Forb	DS	ES	Rock	Bare	Litter	Lichen
S2H4-1	2.2	0.06	57	7	0	35	15	26	3	1	15	7	0	0	8	65
S2H4-2	8.8	0.42	87	31	9	25	22	45	20	7	10	8	0	0	6	46
S2H4-3	7.4	0.82	95	36	11	3	45	32	7	5	5	15	3	0	30	35
S2H5-1	1.4	0.06	43	1	0	20	22	21	1	1	12	7	6	4	4	65
S2H5-2	0.8	0.02	44	1	1	33	9	34	1	2	25	6	15	0.5	2	45
S2H5-3	3.2	0.02	55	7	10	25	13	37	5	2	20	10	20	6	7	30
S3H1-1	1.2	0.1	60	4	10	15	31	43.8	0.2	5.6	5	33	20	1	10	22
S3H1-2	1.2	0.07	59	0	1	31	27	26	0	3	15	8	20	0.1	5	50
S3H1-3	1	0.05	61	4	10	8	39	44.5	2.2	5.3	5	32	7	5	6	37
S3H2-1	0.8	0.13	66	16	9	19	22	50.8	9	3.3	20.5	18	7	1	8	29
S3H2-2	2.4	0.15	89	28	3	17	41	51.7	8.6	2.1	15	26	4	1	12	23
S3H2-3	0.6	0.09	16	16	0	0	0	14	8.7	0.6	4.2	0.5	1	0	10	70
S3H3-1	18.6	2.39	249	50	24	161	14	54	10	6	35	3	0	0	40	5
S3H3-2	26.6	2.26	295	97	6	192	0	71	15	1	55	0	0	0	25	4
S3H3-3	23.4	2.51	440	92	23	325	0	74	10	4	60	0	0	0	20	6
S3H4-1	7.2	0.44	116	80	23	12	1	51.1	15	21	15	0.1	0	0	10	40
S3H4-2	12.6	0.35	187	125	60	0	2	40.6	15	25	0.5	0.1	2	5	27	20
S3H4-3	14.2	0.46	46	36	9	0	1	18.1	10	8	0	0.1	0.5	0.5	15	65
S3H5-1	8.6	0.32	86	30	2	49	5	28.1	7	1	20	0.1	13	13	6	35
S3H5-2	1	0.02	58	19	3	7	29	19	4	1	4	10	40	30	3	10
S3H5-3	0.2	0.1	39	7	4	16	12	13	3	1	4	5	15	25	2	40
S4H1-1	2	0.18	73	13	16	0	44	52	4	8	0	40	8	0	5	35
S4H1-2	1	0.22	52	2	19	20	11	31	4	10	8	9	8	0	7	55
S4H1-3	1.2	0.17	66	4	20	27	15	38.5	4	10.5	16	8	9	2	6	40.5
S4H2-1	2.2	0.06	57	10	0	5	42	30	4	0.5	0.5	25	0	0	5	60
S4H2-2	0.4	0.08	21	11	2	1	7	17	7	3	2	5	9	0.1	5	70
S4H2-3	3.4	0.03	53	23	4	26	0	30	10	6	14	0	0	0	5	65

Plot ID	CH (cm)	LAI	Point Intercept Hits					Percent Cover (%)								
			TV	Gram	Forb	DS	ES	TV	Gram	Forb	DS	ES	Rock	Bare	Litter	Lichen
S4H3-1	15.6	1.08	225	20	12	129	64	61	4	2	45	10	0	0	7	32
S4H3-2	27	1.78	232	113	0	115	4	57	15	1	40	1	0	0	30	13
S4H3-3	19.6	2.14	264	31	0	226	7	76	5	0	70	1	1	0	15	9
S4H4-1	3.8	0.09	79	1	0	4	74	49.1	1	0.1	3	45	0	2	30	15
S4H4-2	6.4	0.45	51	11	1	6	33	39	10	2	2	25	1	0	35	20
S4H4-3	5.6	0.32	50	5	1	0	44	32.6	7	0.1	0.5	25	3	0	18	50
S4H5-1	1	0.04	17	3	0	0	14	13.2	3	0.1	0.1	10	20	3	3	60
S4H5-2	0.6	0.05	20	1	1	7	11	13.1	1	0.1	4	8	25	1	5	55
S4H5-3	1.8	0.02	16	5	0	0	11	9.1	4	0.1	0	5	25	20	5	40

7.0 APPENDIX B: SOIL TEMPERATURE GRADIENT

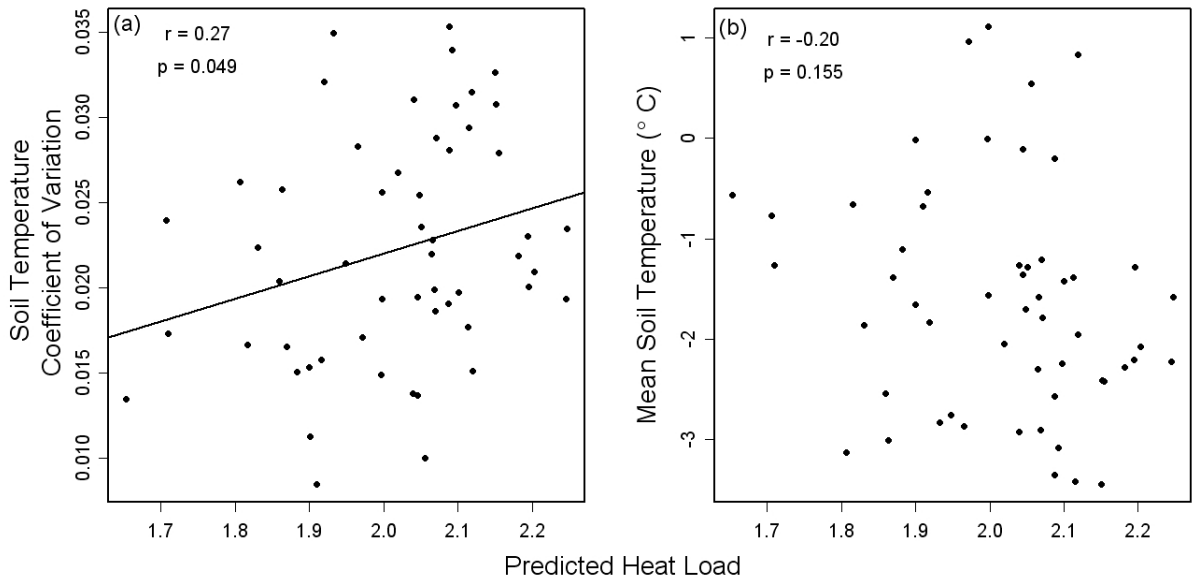

Figure B.1: Bivariate relationships between soil temperature measurements, (a) coefficient of variation and (b) mean temperature, and predicted heat load (n = 54).

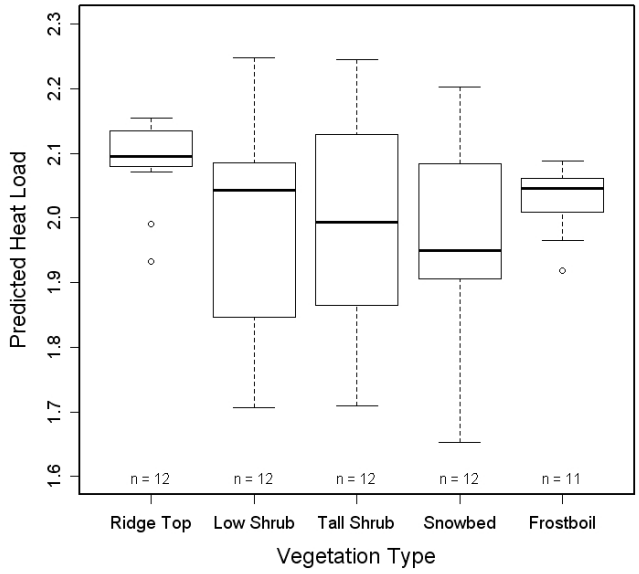

Figure B.2: Predicted heat load as a function of vegetation type classification. There was no significant difference between groups ($F_{4,54}$ = 1.51, p = 0.212). The centre line represents the median, the boxes contain the 25th-75th quartiles of the data, and the whiskers extends to the most extreme data point that is less than 1.5 times the interquartile range with extreme values beyond the whiskers shown as open circles.

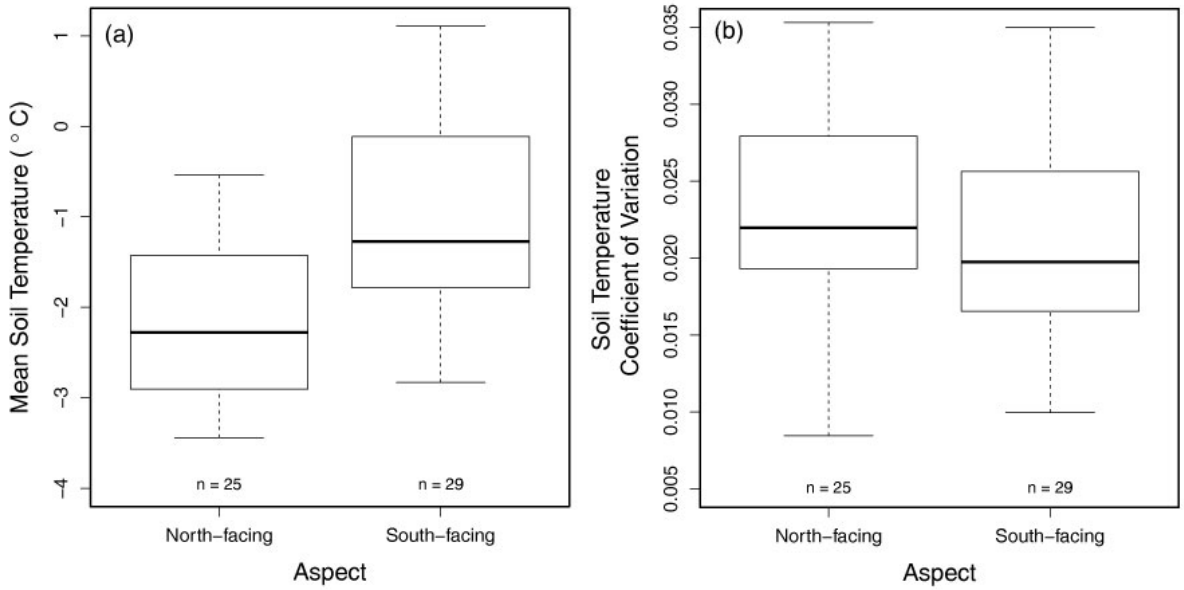

Figure B.3: Soil temperature measurements, (a) mean soil temperature and (b) coefficient of variation, as a function of aspect. Plots located in study areas 1 and 3 are on north-facing slopes while those located in study areas 2 and 4 are on south-facing slopes. The centre line represents the median, the boxes contain the 25^{th}-75^{th} quartiles of the data, and the whiskers extends to the most extreme data point that is less than 1.5 times the interquartile range with extreme values beyond the whiskers shown as open circles.

8.0 APPENDIX C: EXPERIMENTAL STUDY DATA

Table C.1: Summary of experimental study nitrogen data, organized by treatment and block. The 2010 samples are plot level averages of both mineral and organic horizon samples. Abbreviations: treatment combination (Tmt; W = warming, N = fertilization, N+W = warming + fertilization, C = control), and grams dry weight (gdw). See methods section 3.2.3 and 3.2.4 for more information regarding sample collection.

Tmt	Block	Plot ID	2010 Soil Nitrogen[1]			2011 Soil Nitrogen[2]	
			Total Nitrogen[a] (mg N/kg soil)	Nitrate[b] (mg N/kg soil)	Ammonium[b] (mg N/kg soil)	Nitrate[c] (µg N/gdw resin)	Ammonium[c] (µg N/gdw resin)
C	A	A2	8463.7	0.318	30.466	7.15	78.88
	B	B3	7005.2	1.191	21.666	4.07	32.23
	C	C1	7952.4	0.218	25.016	3.37	83.69
	D	D4	5062.3	0.002	9.229	10.96	21.24
	E	E4	7156.5	1.753	17.614	2.88	19.23
	F	F3	11829.6	1.986	20.958	11.66	26.09
N	A	A4	8783.8	1.762	15.618	61.34	15.83
	B	B2	11662.5	1.815	49.016	6.86	48.50
	C	C4	8614.2	0.089	22.685	8.03	15.52
	D	D1	6850.0	0.616	15.905	30.62	72.61
	E	E2	9921.8	0.260	36.503	10.42	43.19
	F	F1	7606.7	0.391	11.921	69.69	65.85
NW	A	A3	8638.6	1.042	23.081	35.62	31.36
	B	B1	3342.4	0.748	8.794	91.15	83.71
	C	C3	5806.5	0.056	10.109	7.10	19.24
	D	D2	4160.8	0.044	7.443	39.81	41.61
	E	E3	5125.2	1.362	8.134	40.91	17.24
	F	F4	6044.0	2.532	10.203	13.72	14.38
W	A	A1	7771.9	1.128	13.399	3.44	84.80
	B	B4	10241.0	2.407	13.542	3.23	22.04
	C	C2	18863.7	0.233	62.543	4.30	44.40
	D	D3	16750.0	0.189	74.375	6.81	19.57
	E	E1	5941.2	1.327	10.436	7.11	72.29
	F	F2	8596.3	0.241	18.663	4.23	36.54

1 – collected from bulk soil samples: a – combustion method, b – KCl extraction & spectrophotometry

2 – collected from ion exchange resins: c – KCl extraction & spectrophotometry

Table C.2: Summary of experimental study leaf data, all measured in mm except number of leaves (leaf #). Plots organized by treatment and then block (see Table C.1). The leaf data was averaged across each plot to get plot level data. Superscript numbers indicate the number of measurements for each species within each plot. See methods section 3.2.3 and 3.2.4 for more information regarding sample collection. Dashes indicate missing data.

Plot ID	*P. viviparum*[5]			*L. arcticus*[5]			*S. arctica*[8]		*S. reticulata*[8]		*D. octopetala*[12]		*C. microchaeta*[8]
	length	width	number	length	width	petiole	length	width	length	width	length	width	length
A2	33.16	5.47	3.8	39.20	8.40	91.80	46.63	18.13	36.75	20.13	15.58	6.83	66.50
B3	20.35	3.59	3.4	25.40	5.20	39.20	39.00	16.50	37.63	19.75	14.42	5.50	-
C1	26.26	4.79	3.8	24.80	5.20	37.60	39.38	15.88	-	-	13.17	4.33	66.00
D4	22.06	3.82	3.4	31.60	7.40	61.00	37.63	12.50	29.25	14.13	13.42	4.83	82.13
E4	24.56	5.00	2.3	25.40	5.20	38.80	31.00	13.13	29.38	14.75	14.00	5.00	60.50
F3	24.28	4.50	3.6	25.00	5.20	38.60	35.38	15.63	25.50	10.63	14.42	5.50	61.63
A4	-	-	-	30.80	5.40	63.20	39.50	15.75	35.13	20.00	12.42	4.50	-
B2	22.42	5.33	2.4	34.80	8.60	59.80	32.38	13.75	32.13	18.38	14.75	6.08	77.63
C4	29.55	5.27	3.7	29.00	6.60	49.80	26.50	9.50	36.88	16.63	15.00	6.42	-
D1	22.15	5.77	2.6	30.40	7.80	70.80	34.63	13.25	31.38	16.88	12.67	4.42	74.25
E2	23.07	4.20	3.0	36.80	8.80	98.20	38.63	16.63	31.00	18.00	14.25	5.75	75.75
F1	23.10	4.30	4.0	29.00	5.60	45.80	38.75	14.25	-	-	13.08	5.17	51.88
A3	28.05	4.68	3.8	35.00	6.40	77.40	-	-	44.13	20.00	12.67	5.67	91.00
B1	23.61	4.89	3.8	34.60	7.40	47.00	42.25	14.75	26.75	14.50	13.83	5.92	94.38
C3	24.27	4.80	3.0	26.00	5.60	47.80	37.50	14.00	30.25	16.38	14.08	5.83	87.50
D2	29.37	5.21	3.8	-	-	-	33.25	13.13	36.25	20.88	14.50	5.42	91.38
E3	22.36	4.36	2.8	27.60	6.80	43.60	38.88	15.25	32.63	15.88	14.42	6.08	68.38
F4	28.09	5.64	4.0	29.80	7.60	67.00	-	-	40.88	15.00	16.83	7.08	77.25
A1	27.31	7.06	3.4	28.80	5.80	45.80	39.25	13.00	39.50	17.13	15.33	6.00	75.00
B4	28.67	5.00	3.0	28.80	6.00	42.60	34.88	13.13	37.63	17.50	15.75	6.25	-
C2	27.83	4.78	3.6	-	-	-	40.88	17.25	35.13	18.25	17.58	7.00	85.00
D3	28.65	4.90	4.0	33.80	7.40	49.40	41.13	19.88	34.13	18.38	15.75	6.33	78.13
E1	23.00	4.40	2.0	32.00	7.60	56.80	35.13	12.88	27.50	12.75	11.33	4.17	47.63
F2	23.11	4.84	3.8	35.40	8.40	77.40	41.75	16.25	32.25	16.25	14.17	6.42	53.75

Table C.3: Summary of experimental study specific leaf area (SLA) data, organized by treatment and block. The SLA data was averaged across each plot to get plot level data. Superscript numbers indicate the number of leaves sampled for each species within each plot. See methods section 3.2.3 and 3.2.4 for more information regarding sample collection. Dashes indicate missing data.

Tmt	Block	Plot ID	*L. arcticus*[5]	*S. arctica*[8]	*S. reticulata*[8]	*D. octopetala*[12]	*C. microchaeta*[8]
C	A	A2	2.669	1.630	1.341	0.962	-
	B	B3	2.514	1.448	1.105	0.898	-
	C	C1	-	1.217	-	0.664	1.115
	D	D4	2.489	1.431	1.164	0.707	1.459
	E	E4	2.319	-	1.053	0.720	1.674
	F	F3	2.710	1.144	-	0.706	1.126
N	A	A4	2.528	1.174	1.226	0.683	-
	B	B2	2.650	-	1.289	0.801	1.332
	C	C4	2.578	-	1.226	0.945	-
	D	D1	1.830	1.365	1.057	0.649	0.960
	E	E2	2.796	-	1.372	0.828	1.071
	F	F1	2.448	1.191	-	0.728	-
NW	A	A3	2.894	-	1.287	0.962	1.282
	B	B1	2.121	1.213	-	0.737	0.811
	C	C3	2.628	1.204	1.211	0.824	1.114
	D	D2	-	-	1.398	0.878	1.192
	E	E3	2.588	1.416	1.104	0.906	1.175
	F	F4	3.613	-	1.080	1.030	1.243
W	A	A1	-	1.203	1.085	0.824	1.084
	B	B4	2.741	1.393	1.023	0.876	-
	C	C2	-	1.325	1.237	0.995	1.170
	D	D3	2.612	1.195	1.089	0.837	1.710
	E	E1	2.403	1.277	0.967	0.625	1.174
	F	F2	2.335	1.256	1.087	0.873	1.098